MASTER THESIS

THE INFLUENCE OF MOOSE (*ALCES ALCES*) ON NUTRIENT DYNAMICS IN A FEN ECOSYSTEM

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Left: Catchment area of Biebrza National Park (source: see references). Right: Moose in the brushwood (photo: Sanne Dirickx).

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“First, therefore I will speak of the Elke, which the Savages call a Mose: it
is a very large Deare, with a very faire head, and a broad palme, like the
palme of a fallow Deares horne, but much bigger, and is 6 footewide
between the tipps, which grow curbing downwards:
he is of the bignesse of a great horse”.

Samuel Champlain, 1603 (in: Merril, 1920)

“By coincidence she saw water in a lake, in the deepest of the valley,
where farmers were collecting rushes, invading the marsh
Latona went down, kneeled and leaned on the soil to take and drink from the water”

(r5, Metamorphoses VI, 339-38)

TABLE OF CONTENTS

PART 1: REMOVAL OF NUTRIENTS BY MOOSE

PART 2: NUTRIENT INPUT IN THE ECOSYSTEM BY MOOSE

PART 3: NUTRIENT UPTAKE BY PLANTS

Introduction

GENERAL DISCUSSION ON NUTRIENT DYNAMICS: SYNTHESIS OF PART 1, 2 AND 3

ABSTRACT

This study investigates the influence of moose (*Alces alces*), a large herbivore, on nutrient dynamics in an undisturbed fen ecosystem. This is of particular interest as mineralisation rates in fen systems are low, offering the potential to moose to enhance the nutrient turnover by short-cutting the decomposition. A nutrient balance of nitrogen (N), the limiting nutrient in Biebrza National Park (BNP), and phosphorus (P) is developed, in order to examine the relevance of moose activities concerning nutrients in the ecosystem. The comparison of the amount of moose's nutrient input with mineralisation rates and atmospheric nutrient deposition is in this respect of major importance. Furthermore, it is investigated whether or not moose re-allocate nutrients by foraging and depositing excretion in different habitats, as often done by herbivores. In addition, the estimated yearly nutrient uptake of the vegetation – affected by an enhanced nutrient turnover – is compared with the total nutrient input. Finally, I discuss whether moose, by suppression or stimulation, may cause a shift in specific plant communities or species.

This study indicates that moose have a substantial impact on N dynamics, specifically in undrained sites. Moose cause no nutrient redistribution but generate a local recycling of nutrients in the brushwood, dominated by willows and birches, instead. As a consequence, moose may stimulate brushwood expansion, in spite of the mechanical damage caused. This stimulatory effect contrasts with the often supposed role of moose in suppressing forestation. As this study demonstrates, moose may not be considered as an appropriate restoration tool to suppress ongoing shrub encroachment in BNP.

GENERAL INTRODUCTION

Nutrient dynamics imply fluxes of nutrients moving from one compartment to another (Fig.1), the rate of which is described by nutrient turnover rate (Begon *et al.*, 2009). At low turnover rates, nutrients are essentially stored for a long time, at high rates they quickly become available. At low turnover rates, herbivores have potentially the largest effect on nutrient dynamics (Sjögersten *et al.*, 2010). Examples could include nutrient cycling in undisturbed fen ecosystems, because these are characterised by a very low mineralisation rate (Van der Linden *et al.*, 1996; Riutta, 2008; Olde Venterink *et al.*, 2009). Consequently, external inputs may change the cycling rate but not the cycle itself (Bokdam, 2001).

A fen is partly fed by groundwater and partly by surface water (Vandenbussche *et al.*, 2002). The water level is at or very close to the surface level throughout the year (Hermy *et al.*, 2004), leading to anoxic conditions (Van der Linden *et al.*, 1996) and a very low decomposition rate (Chapin *et al.*, 2003). As a consequence, in the long term, nutrients are sequestrated in persistent organic material, called peat (Chapin *et al.*, 2003; Riutta, 2008).

Herbivores can accelerate nutrient cycling directly by short-cutting the decomposition process (Van der Wal & Brooker, 2004). They transfer nutrients from their forage into urinary and faecal excretion. Nutrient recycling by this process is normally much faster than the turnover rate of litter (Van der Wal & Brooker, 2004). Moreover, selective foraging by large herbivores may result in a redistribution of nutrients from the forage habitat to the resting places if these are separated (Bokdam, 2001; Mouissie *et al.*, 2005).

Moose (*Alces alces*) is the largest herbivore adapted to fen ecosystems (MacDonald & Barrett, 1993; Baskin & Danell, 2003) and the present study investigates its effects on nutrient dynamics therein. In this way a nutrient flow is created, impoverishing the forage species and enriching the vegetation type used to rest. Selective foraging by moose was found to alter species and community composition (Alldredge *et al.*, 2001; Tschöpe *et al.*, 2011), vegetation structure (Pastor *et al.*, 1993) and successional patterns (Tschöpe *et al.*, 2011). Moose are able to suppress the growth (Bergström & Danell, 1995; Abaturov & Smirnov, 2002; Heikkilä *et al.*, 2003; Persson *et al.*, 2003b; Dungan & Wright, 2005) and the productivity (Pastor *et al.*, 1988; Alldredge *et al.*, 2001) of certain species by browsing them. The degree of suppression depends on the regenerative ability of the species foraged upon and is higher at higher moose densities (Abaturov & Smirnov, 2002). Moreover, several authors assume that moose are able to slow down shrub encroachment (Schmidt *et al.*, 2000; Alldredge *et al.*, 2001; Van Assche, 2001; Middleton *et al.*, 2006). At the same time, other authors, who work mainly in the Arctic, find a totally different effect and instead describe a stimulation of plant production by herbivore excretions (Van der Wal & Brooker, 2004; Van der Graaf *et al.*, 2005).

Wheeler & Proctor (2000) and Økland *et al.* (2001) consider hydrological dynamics and nutrient availability as the main factors controlling vegetation performance in peatlands. Nitrogen (N), phosphorus (P) and potassium (K) are macronutrients, essential elements for plant growth that are required in large amounts (Raven *et al.*, 2003). Olde Venterink *et al.* (2009) showed that in the fen system, the Biebrza National Park, N is the limiting nutrient that restricts vegetation growth, as is the case in most central European fens (Koerselman & Verhoeven, 1995). The effect of moose on the recycling of N and P is the subject of the present study. The abbreviations N and P will be used throughout this study to describe nitrogen respectively phosphorus compounds, although they may refer to different chemical compounds in different conditions.

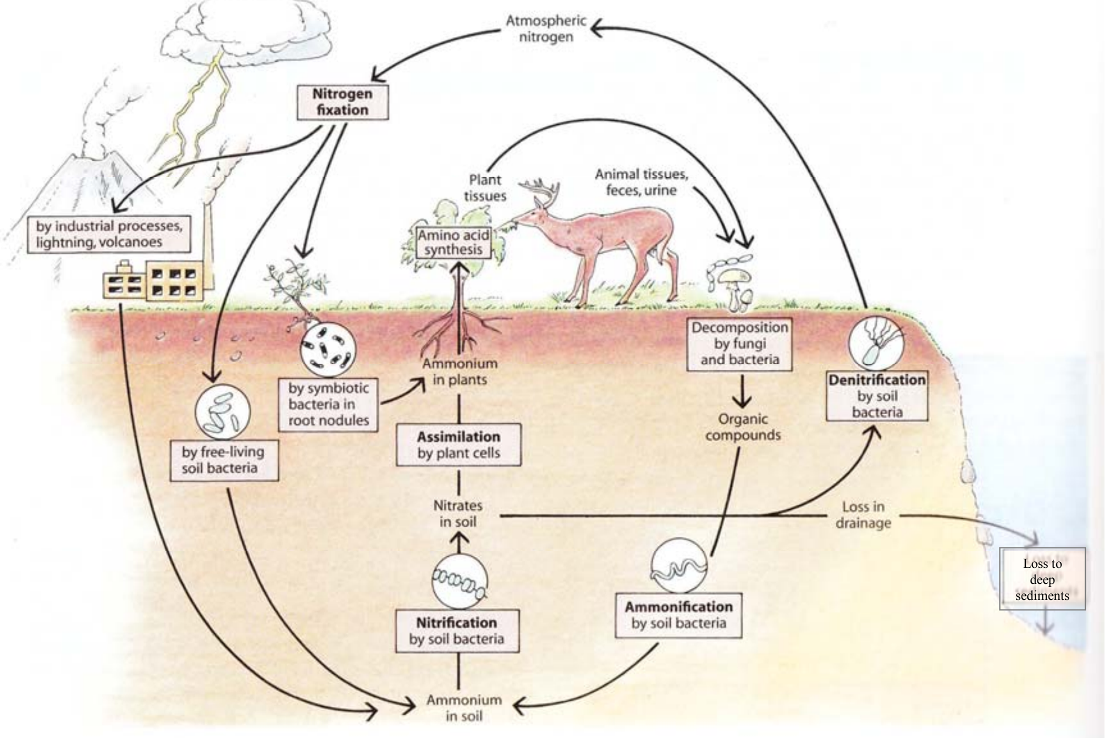


Fig. 1: The nitrogen cycle in a terrestrial ecosystem (fig. from Raven *et al.*, 2003).

AIM OF THE STUDY

The aim of the present study is to investigate the *direct* effects of moose on the nutrient dynamics of a fen ecosystem, which is of specific interest as nutrient availability (mainly N) is low, limiting plant growth. To investigate whether or not moose redistribute nutrients in the ecosystem, this study discusses from which parts of the ecosystem nutrients are removed and in which parts moose cause an enhanced nutrient availability by excretion. Further, the main research question, the relevance of moose on the ecosystem in terms of quantities, is investigated. In order to assess the relevance of moose activity, the *amount* of nutrients removed from the system is compared to the *amount* of input by excretion. The relevance of the amount of input by moose is also compared to soil mineralisation rates. Total nutrient input (excretion of moose, soil mineralization and atmospheric deposition) is compared to the estimated amount of nutrients taken up yearly by the vegetation. Finally, it is discussed whether or not moose suppress or stimulate specific plant communities or species.

GENERAL HYPOTHESES

I hypothesise that moose have a substantial impact on the nutrient dynamics of a fen ecosystem by enhancing nutrient turnover. Firstly, moose are expected to re-allocate nutrients from forage areas to resting places. Secondly, the amount of nitrogen (N) deposited by moose is assumed to be substantial in this N limited ecosystem. Thirdly, I hypothesise that this re-allocation leads to the enhancement of production in the resting places and to a growth suppression at the foraging sites.

STRUCTURE OF THE STUDY

The study discusses three key factors of the nutrient cycle that are affected by moose (Fig.2). Part 1, *removal of nutrients by moose* and part 2, *input of nutrients by moose*, are discussed in more detail than part 3, *uptake of nutrients by existing vegetation*, as the latter is rather stated as a hypothesis and is not supported by a large amount of data. In the general discussion, the three parts are linked and the relative impact of moose on the total nutrient balance is assessed. Removal, input and uptake were only looked at in the relevant growth season for plants (indicated as yearly), excluding winter.

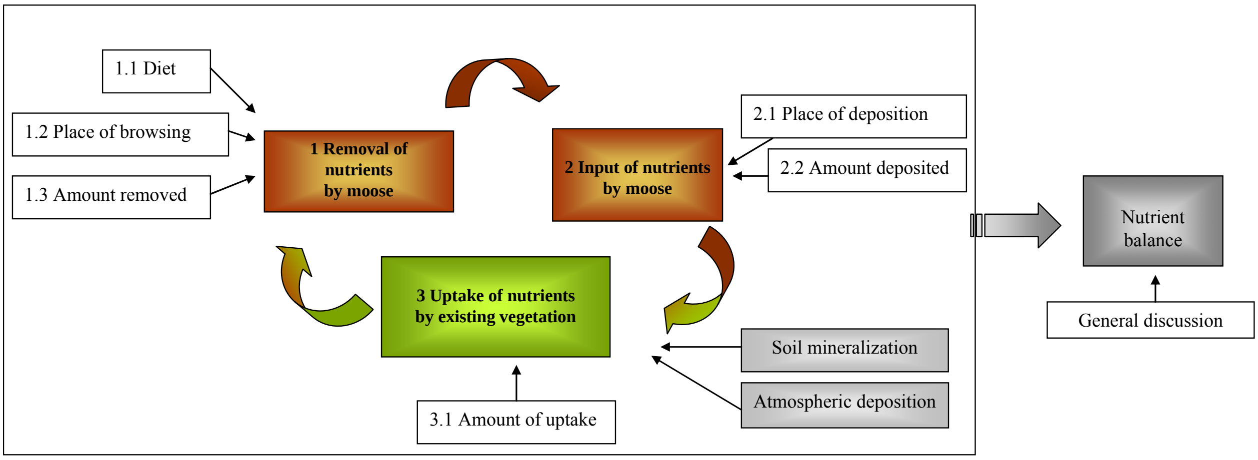


Fig. 2: Nutrient cycle in an ecosystem by intervention of moose (*Alces alces*): the three parts considered.

NUMERICAL ANALYSES

Calculations were performed with Microsoft Excel, version 2003. Statistical analyses were carried out with the statistical programme R, version 2.7.2. Differences giving a p-value lower than 0.05 were considered as significant.

STUDY SITE

The study site is situated in the Biebrza National Park (BNP), in NE-Poland (Fig. I.27:). The BNP is one of the best preserved wetland areas in Europe, often considered as a reference for natural wetlands (Schmidt *et al.*, 2000). The area consists of a large fen ecosystem and a small bog area. The park was established in 1993, and designated a Ramsar site in 1995 (Schmidt *et al.*, 2000) and is included in the EU Natura 2000 network (pers. inf. Kotowki W., 2010). This ecosystem is particularly important because of its high biodiversity and water and carbon storage capacity (Joosten & Clarke, 2002; Dabrowska-Zielinska *et al.*, 2009). Nevertheless, the Biebrza NP struggles since 1960 with shrub (willow and birch) encroachment (Bokdam *et al.*, 2002), threatening biodiversity (Schmidt *et al.*, 2000) (Appendix IX). This shrub encroachment is caused by cessation of agricultural management, resulting in a spontaneous afforestation (Schmidt *et al.*, 2000; Middleton *et al.*, 2006), accelerated by a change in climate (Schmidt *et al.*, 2000) and hydrology (Schmidt *et al.*, 2000; Bokdam *et al.*, 2002 ref). In 2005, mowing and brush chopping were started with a view to restoring species-rich open fens (ref).

The mean annual temperature is 7°C (Kossowowska-Cezak & Olszewski, 1991 in: Schmidt *et al.*, 2000). The mean monthly summer air temperature is 17-19°C and the humidity is high but varies strongly within the area (Schmidt *et al.*, 2000). The mean annual insolation ranges between 3.6 and 4.8 hours per day (Kossowowska-Cezak & Olszewski, 1991 in: Schmidt *et al.*, 2000) and the annual rainfall is 650mm. A severe winter (with snow cover) may last for over 4 months (Schmidt *et al.*, 2000), the vegetation growing season is therefore short (www.biebrza.org), approximately 7 months. The river valley is formed in the Pleistocene period (Schmidt *et al.*, 2000). Based on the geomorphology, the park can be divided in three relatively isolated parts (Schmidt *et al.*, 2000): the upper or northern basin, the middle basin and the lower or southern basin. Most of the field work was carried out in the southern basin, a smaller part in the middle basin and few data were collected in the upper basin (Fig.I.27). The field work was performed from July until the middle of September (summer and early fall) of 2010, in spring (April) 2011 and in the summer (end of June, beginning of July) of 2011. Field work only took place in the fen area, but was also partly carried out close to the bog area.

The BNP can be divided in zones, following one upon each other, in a typical sequence (Klosowski *et al.*, 2009). The mineral part of the valley edge is covered by coniferous forest, which turns gradually into a zone of alder (or alder-birch) carr and then into a belt of willow shrub. Those are gradually replaced by birch shrub and strips of open birch forest. The next vegetation zone consists of large sedges that turn into reed belts along the river bank (Klosowski *et al.*, 2009) (Fig. IX.42).

STUDY SPECIES

The study species, moose (*Alces alces*), is one of the largest herbivores in Europe (MacDonald & Barrett, 1993), specifically adapted to wetland areas as a summer habitat (Raczyński & Gębczyńska, 1990). Yet, when winter loom moose often migrate to more forested areas (MacCracken *et al.*, 1997; Bobek *et al.*, 2005; Stumph &Wright, 2007). At the same time, moose give up their solitary life and gather in small groups (Baskin and Danell, 2003). Moose are ruminants, mostly considered to browse, which is "to eat tender parts of woody plants such as leaves and shoots" (Lawrence, 2000). A mean annual home range of around 59km² is actively used by moose (MacCracken *et al.*, 1997). Yet, females and males show different home range sizes and acitivity patterns (Neumann *et al.*, 2009). Calves are given birth in the marshes and stay at their mothers' side, almost until the next calf is born. In BNP, moose have a natural predator, the wolf (*Canis lupus*). Three wolf packs of approximately 20 individuals roam in BNP (pers. inf. Kotowski K., 2011). Moose have a special status in BNP, partially due to a small moose population that survived World War II in the bog area of BNP and developed into a large population thereafter, spreading in Poland (Raczyński & Gębczyńska, 1990).

Alces alces is called "moose" in the United States, but is originally called "elk" in Europe (MacDonald & Barrett, 1993). Nonetheless, this study uses "moose" to avoid confusion with *Cervus elaphus*, which is, at its turn, called "elk" in the United States.

PART 1: REMOVAL OF NUTRIENTS BY MOOSE

Introduction

The main goal of this part is to assess the amount of nutrients removed by moose. Therefore, the diet of moose has to be known, to assess subsequently from *which* plants nutrients are removed. Namely, the proportions of plant categories consumed by moose and specifically the species browsed and grazed have to be determined (§1.1.1), as no specific study in BNP has been carried out yet concerning diet. There are a number of methods to estimate diet: by following moose tracks (Routledge & Roese, 2004) or paths (Shipley *et al.*, 1998), by observations (Dungan & Wright, 2005), microscopic diet analysis (Dungan & Wright, 2005; Kuijper *et al.*, 2008 and 2009; Jayakody *et al.*, 2011) and by counting grazing signs in plots (Kuijper *et al.*, 2009). They all have their advantages and drawbacks. Therefore, we approached the diet of moose, using two methods and we compared the results. Firstly, browsed and grazed plant species on transects were counted (§1.1.1A) and secondly, pellets were microscopically analysed (§1.1.1B). Furthermore, as data on moose consumption, collected on transects, may include signs of other ungulates, few specific data has been collected on red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) to get some additional information that might help to assign the browsing data to the right species' diet (§1.1.3). Unbrowsed and ungrazed plants were counted as well on transects, making it possible to figure out whether moose browse and graze *selectively* on certain species or not, as this might indicate that nutrient removal occurs not randomly (§1.1.2). Next to this, the preferred plant height and water level to consume food was assessed. The former is interesting to determine if moose have a preference related to vegetation structure. The latter may be interesting to link the places were biomass is removed with a certain decomposition rate, at its turn linked to water level (Van der Linden *et al.*, 1996). It is expected that moose consume their food preferably at a certain "comfortable" height and in any water level (MacDonald & Barrett, 1993). Furthermore, it is revealed in *which* vegetation types moose remove nutrients by comparing percentages of plant species consumed in different structural vegetation types (§1.2). Finally, the *amount* of nutrients in the consumed parts of the forage species is estimated (§1.3). In addition, a short supplement on winter diet is enclosed (Appendix VII).

Method

1.1 Diet of moose in summer

1.1.1A Transect data

Moose diet of *large ungulates* has been estimated by counting browsed and unbrowsed plants (Kuijper *et al.*, 2009) on transects orientating with Global Positioning System (GPS) and compass (further on in this study the method, here explained, is referred to as "transect method"). Transects were chosen, as this allowed to investigate a combination of diet composition (§1.1.1) and selectivity (§1.1.2), habitat preference (§1.2.2) and place of nutrient deposition (§2.1), at once. To enhance the chance to estimate *moose* diet in particular, sites with high moose densities were chosen. These were based on observational data on moose densities in BNP (Fig.I.28). Vegetation was classified according to their main structure in five structural vegetation types: coniferous forest, brook forest, brushwood, sedge marsh and reed marsh. In each structural vegetation type at least 500m of transects have been walked. (Table 1.1; Fig. I.28) Overall, 77 transects (60 in the lower and 17 in the middle basin), each of around 100 metres long and one metre wide, have been walked (in total 6242m²). Beginning and end coordinate of the transect were marked with GPS and the transect was tracked. The transects were spread over the study area to get a representative picture of the general moose diet in the area. Transects of *different* structural vegetation types were walked in a random order to overcome a time effect. For each tree and shrub on the transect and when possible for sedges and herbs, it was listed whether they were browsed or grazed or not. Individuals were identified at the level of species when possible (Rothmaler, 1994a and 1994b; Heimans *et al.*, 1996; Eggelte, 2006).

On the basis of the rough transect data, numbers of browsed individuals were summed per plant species, per transect and per structural vegetation type. As the transects investigated had a different area, the numbers counted had to be treated according to their distance. Data were multiplied by a weigh factor (number of metres per transect divided by the total number examined per structural vegetation type). These weighed numbers were summed per plant and per transect. Finally, the mean number of browsed or grazed individuals per plant category were divided by the total number of browsed individuals. Fractions are shown in pie diagrams (Fig. 1.3A). These data were normally distributed and a one-way ANOVA was used to find out if plant categories were unequally represented in the moose diet. A Tukey Honestly Significant Difference (HSD) was accomplished to find out which plant categories (independent variable) were significantly different from each other concerning browse percentage (dependent variable).

Table 1.1: Structural vegetation types: area of transects (m²) and number of transects.

Structural vegetation types	Area of transects (m²)	Number of transects
Brushwood	2656	31
Brook forest	1276	19
Sedge marsh	1177	11
Coniferous forest	547	5
Reed marsh	546	11
Over all	6202	77

1.1.1B Microscopic diet analysis

A microscopic diet analysis was carried out to estimate the diet of moose, in particular excluding red and roe deer. Sub-samples were microscopically analysed to find out the diet composition of moose based on epidermal fragments of partly digested plants. Fresh pellets (Fig.I.28; II.32; II.33) were randomly collected on transects (§ 1.1.1A) from the beginning till the end of August. Additional samples were collected specifically in structural vegetation types preferred for browsing (§ 1.2) and for deposition of pellets (§ 2.1) and in areas where moose had recently been seen. These were places with high concentrations of willow shrubs, in birch stands and on edges of alder forests. In these areas (lower, middle and upper basin) samples were taken by walking in random directions. The period of gathering was between the end of August (28, 29, 31) and the beginning of September (1, 4, 5, 11) of the year 2010.

Samples consisted of approximately 7-10 pellets or of the estimated volume of 7-10 pellets, when pellets were undistinguishable as a result of the pellets being often diarrhoea. Some samples may originate from the same individual moose. Yet, differences in size of pellets and pellet heaps, indicate young, female and male moose samples. At each location pellet size was considered, to take samples of as many different individuals as possible. Pellets were collected at seven locations (Fig. I.30). In total, 70 pellet samples of moose were collected, of which 55 samples were gathered in brushwood, 6 samples in alder carr and 9 samples on edges between brushwood and alder carr. From red deer and roe deer respectively 5 and 4 pellet samples were gathered, spread over time and spatially spread over the lower basin (Fig. I.30). Pellet samples were collected in plastic bags of 3 litre and put in porous paper bags afterwards. After maximum two days they were put in a stove (Premed KBC G-65/250) for drying to optimally conserve and transport them. The samples were dried at 70°C for several days, the duration depending on the amount of samples and the content of water. They were all extra dried before transport. Finally, they were put in a freezer at -18°C to stop the growth of fungi, occurring on 1/4th of the samples, since the extraction system of the oven had not been functioning well. This might cause some plant fragments to be damaged, which has to be considered when performing the microscopic analysis of the pellets.

A reference collection was made from 24 different species and from groups of species characterised together (Appendix X). The species were chosen according to the species that were browsed most frequently in the field, resulting from the transect data. In addition, also grasses, sedges, reed, herbs, trees and shrubs frequently occurring in the area but not especially selected by moose resulting from the transect data, were sampled to be able to correct for underestimations in the study field. Leaves were collected in BNP, except for samples of mosses, that were collected in Belgium. Leaves of the species were collected in the study area from at least three individuals. The epidermis was pulled off at different places of the leafs, on upper and back side, on the edge and in the middle (Kuijper *et al.*, 2009). The epidermis is namely the part that remains undigested and is as such used to recognise plant species in pellets (Kuijper *et al.*, 2008 and 2009b). For many species, a preparing procedure (Fig.II.34) was needed to be able to pull off parts of the epidermis. *Soft* leaves rather needed steaming or soaking in natural soap (Biały jeleń) or a combination of both. The epidermis of *tough* leaves could sometimes be scraped with a knife or treated with ecological detergent (Sidolux) or bleach water (12° Cl; 39.92 g/l NaOCl) or a combination of those. However, the latter treatment with bleach water needed however to be short (around 20 minutes) to ensure that the cell walls were not broken. As such, cells would not be recognisable anymore. Per species minimum one microscopic slide (composed of epidermises of some individuals) was made, sealed with transparent nail polish. The microscopic analysis as a whole took three months time. The microscopic slides were studied to be able to recognise species in the pellet samples. For each species or group of species, important characteristics were listed, looking at: cell form and size (length); form, size and density of the stomata; number of cells around the stomata and other peculiarities (Appendix X; de Jong, 2006). Photographs of the reference collection were made by an Olympus BX50 C-4040 zoom, F 1.8 and by a Canon 1000D, EFS 18-55mm.

Per pellet sample a representative subsample was taken and the following procedure was accomplished. Large twig fragments were crushed by a spoon, whereafter the sub-sample was grinded to fine dust in a mixer (Tomado, TM-1287). This caused cell fragments to be thin enough to be able to see monolayers of cells. A small part was further mixed with 3mL of tap water and 6mL of bleach water (12° Cl; 39.92 g/L NaOCl) and the fragments were soaked for one hour. However, for red and roe deer samples the duration of soaking was only 15 minutes. This duration was experimentally determined as the point to destroy the chlorophyll in the mesophyll layer by bleaching. This enlarged the visibility of individual cells, but leaving the cell walls intact. Then, the emulsion was poured through a colander with holes of 0.125 x 0.125 mm. The part that was gone through consisted of fragments that were too small to determine. The remaining parts were put in a Petri dish abd a little tap water was added. From this emulsion a drop with fragments was put on a microscopic slide and a cover glass was put on top of it. The line-intercept method (Seber and Pemberton, 1979; Gebzynska and Myrcha 1996 in: Kuijper, 2009) was used, with identification of only fragments in the centre of the microscopic field (Owen, 1975 in: Kuijper, 2009). The microscopic slide was diagonally studied by moving it successive steps of 2mm up and to the right (Kuijper, 2009). As such, the distance between two sample points within the slide was larger than that of the size of plant fragments. This resulted in 10 randomly identified plant fragments per sub-sample (Kuijper, 2009). Every fragment was studied and identified at species-level if possible, otherwise it was assigned to a category ("grasses, sedges and reed", "herbs", "wood", "mosses" and "veins") (Table 1.2). Of monocotyledons, rather groups were characterised in stead of (as opposed) species. When it was not clear whether a plant fragment belonged to herbs or to wood, it was noted as "dicotyl". Fragments that could not be assigned to one of the categories were listed as "unknown". Identification was done with help of the reference collection made and the reference collection of Emilia Hofman (pers. inf., 2010). Per mixed pellet sample, 10 microscopic samples were studied resulting in 100 randomly identified plant fragments per sample (Kuijper, 2009).

Based on data of the diet analysis, the number of fragments per plant species and per plant category per sample was counted. Percentages per plant category were calculated based on means over all samples (Fig. 1.3 B1; Fig. 1.4 A1; Fig. 1.4 B1). As the veins could not be assigned to or divided over the categories, they were excluded in the next phase, assuming that they could be distributed evenly over all categories. Therefore, the mean percentages were divided by the new total (without the percentage of veins) (Fig. 1.3: B2; Fig. 1.4: A2, B2). As the microscopic data were percentages, which have a rather binominal than a normal distribution, an arcsine transformation was used (Zar, 1999) prior to further analysis. As such a parametric one-way ANOVA and Tukey (HSD) was used to test for differences in browse percentages (dependent variable) between the plant categories (independent variable).

1.1.2 Diet selectivity by moose

A Jacobs selectivity index was calculated to show whether there is selectivity for one or more species and if this is the case, which species are positively (+1) and negatively (-1) selected for, this means the latter being avoided (Jacobs, 1974). The following formula (formula 1.1) was applied to calculate the index:

Jacobs selectivity index = $D = (r-p)/(r+p-2rp)$ (formula 1.1) (Jacobs, 1974).

In concrete, the index relates the proportion of a species *browsed* (r) in relation to the proportion of a species *occurring* (p). Occurrences of plant species were had been assessed on transects as browsed and unbrowsed individuals were counted. Occurrences of reed, sedges and herbs were estimated by counting the number of metres of these groups and multiplying them by 100 (which is the estimated number per metre). For each plant category a Jacobs selectivity index was calculated. Per transect the weighed numbers of occurrence were summed per category. Then the mean was calculated over all transects per category. The proportion of *occurring* individuals (p) was calculated by dividing these means by the mean total number of individuals that occurred counted over *all* transects (Fig. 1.5). The same reasoning was followed to calculate the proportion of *browsed* individuals (r). Then the index was calculated as in formula 1.1. (Fig. 1.5, A1). Based on the microscopic data, the same index was calculated, using proportions of occurrences from the transect data (Fig. 1.5 A2). As trees seemed to be the preferred category, a Jacobs selectivity index was calculated only for tree species to provide information on which tree species were preferred in relation to the tree species occurring (Fig. 1.5 C1 and C2).

1.1.3 Comparison of the moose diet with other ungulate species

Because data of red and roe deer samples were percentages, being not normally distributed, they were arcsine transformed. Two-way ANOVAs, with fixed factors (plant category and ungulate species) were conducted between moose and red deer, moose and roe deer and red and roe deer. Percentages (proportions) browsed were used as dependent variable. It was also tested whether or not there was an interaction between percentage browsed and plant categories. Tukey (HSD) tests were used to determine the differences between the species within the categories. An interaction plot was made with a view to visualising the comparison of the species (Fig. 1.6 and Table 1.3 and 1.4).

1.1.4 Comparison of the methods

To be able to compare the transect data with the microscopic data, the former needed to be arcsine transformed as was needed for the latter. A two-way ANOVA, with fixed factors, ungulate species and category, was conducted as I was specifically interested in differences in diet (dependent variable) between the two mentioned methods as well as in the plant categories specifically. It was also tested whether there was an interaction between percentage browsed and plant categories. A Tukey (HSD) was used to show the differences in browse percentages between the methods within the categories. An interaction plot was made, to visualise the comparison of the methods (Fig. 1.7 and Table 1.5).

1.1.5 Is there a link between browsing frequency and plant height and water level?

Summed data over all transects were used to look for correlations between several variables. Individual plants were assigned to categories by *estimating* their height and the water level at their location (always performed by the same person). Each individual plant on the transects was placed in a height category (4 categories: < 0.8m; 0.8m - 2m; 2m - 5m; >5m). The first category contains mostly seedlings of trees and shrubs and small herbs, grasses and sedges (herb, grass sedge and reed seedlings were not taken into account); "0.8m – 2m" are small trees and shrubs and most herbs and sedges; "2m - 5m" are mostly young trees;" > 6m" are mostly old trees. The water level was indicated by an estimated gradient (< 10cm, 10cm – 30cm; 30cm – 50cm; > 50cm) at the location of the plant. In order to look at correlations, a biplot (Fig. 1.8) was made, based on a Principal Component Analysis (PCA). Five variables were used: browsing (0 or 1), plant species, plant height, water level and structural vegetation type. Besides, the influence of plant height and water level on browsing percentage over *all* species was looked at in more detail Fig. 1.9). Considering selectivity within tree species, for three positive and three negative selected plant species (Fig.IV.36, Fig.IV.37). The number of individuals occurring in each category was given as well to get additional information on abundances per category. Chi-squared (χ^2) tests were applied to test for differences between categories. Observed frequencies were compared with expected frequencies. Hereby, it was expected that browse frequency on the one hand and the number of individuals occurring on the other hand were equal in all height categories. Expected frequencies were found by summing the observed frequencies and dividing them equally over the categories.

1.2 Place of nutrient removal

To consider the use of structural vegetation types, the *total* percentage browsed, in relation to the number of plant individuals occurring, within each structural vegetation type was given (Fig. 1.10). For each structural vegetation type, percentages browsed of the proportion occurring of each *plant category* in each type are given (Fig. 1.11 A). As deciduous shrubs are the main food for moose, graphs with percentages browsed of tree species per structural vegetation types were made (Fig. 1.11 B1-B4), showing the species occurring and their proportion in relation to the other species within the type occurring. To assess a probable importance of the location of brushwood in the ecosystem, an extra 500 metres of transects were investigated for brushwood, connected to a forested type, to compare with brushwood "islands". Browsing percentages of tree species were put in a graph to compare (Fig 1.12). All data, consist of percentages and were arc sine transformed. One-way ANOVAs and Tukey (HSD) were used to test for differences between (sub)structural vegetation types (Appendix VI).

1.3 Amount of nutrients removed by moose

1.3.1 Moose density

An estimation of 600 moose in BNP (pers. inf Kotowski W., 2010) over an area of 170 000 ha (Gebczyńska & Raczyński, 1993 in: Borkowska & Konopko, 1994) (Table III.16) was used to estimate moose density. This area comprises the park without surrounding forests, as the latter seem not to be frequent habitat for moose in summer (Appendix VII). This results in a moose density of (600 moose/170000ha) 3 moose*1000ha^{-1}, a general moose density, in the park. However, moose are not evenly spread over this area. In the area where moose are commonly seen (Table IV.2), I used a moose density of 10 moose*1000ha^{-1} (Gebczyńska & Raczyński, 1984; pers. inf. Kotowski W., 2010). Based on pellet densities, the moose density in the brushwood was estimated to be three times higher than elsewhere. This results in a moose density of 30 moose*1000ha^{-1}.

1.3.2 Biomass removal by moose

Daily food intake per moose was estimated to 10kg dry mass in summer (Persson *et al.*, 2000; Persson *et al.*, 2003) (Table III.13). The biomass intake of dry mass in summer over the whole park area is (summer: 7 months from April to October) (www.biebrza.org.pl, 2011) is (10kg * 214 days * 3 moose*1000ha^{-1}) 6.4 kgDM*ha^{-1}*yr^{-1} (DM = dry mass) or in places where moose occur in higher densities (10kg DM* 214 days 10 moose*1000ha^{-1}) is 21.4 kgDM*ha^{-1}*yr^{-1}. In the brushwood (10kg * 214 days * 30 moose*1000ha^{-1}) 64 kgDM*ha^{-1}*yr^{-1} was removed.

1.3.3 Amount of nutrients removed from the browse species

Firstly the biomass removal was calculated per plant species, using the percentage that the species contributes to the diet (Perc) and the amount of biomass (kg*ha^{-1}*yr^{-1}) removed by moose: (Appendix III)

$\text{Perc}_{\textit{Salix cinerea}}$ (%)*$M_{\text{totalbiomass}}$ (kg*ha^{-1}*yr^{-1}) (formula 1.2)

A *Salix cinerea*

N and P content of twigs and leaves of *Salix cinerea* was analysed, as moose browse mainly on these fresh parts (Lawrence, 2000; Bergström & Guillet, 2002) resulting from primary growth (Raven *et al.*, 2003). Samples were taken in the end of June 2011 from four sites. Two or four shrubs per site (12 shrubs in total) were randomly picked out to sample (more details in §5.1). Twigs of less than one year old and leaves were sampled, the latter evidently being maximum one year old as *Salix cinerea* is deciduous. The amount of nutrients removed from *Salix cinerea* was calculated by:

(M_{Nuleaf}(g/kg)*2 + $M_{\text{Nutwig,<1year}}$(g/kg)) * BRsp (Formula 1.3)

M_{Nuleaf} is the mean amount of nutrient (N or P) (g*kg^{-1} leaf); $M_{\text{Nutwig,<1year}}$ is the mean amount of nutrient (N or P) (g*kg^{-1} twig of less than one year old); BRsp is the biomass removal calculated per plant species.

B. Other deciduous tree species

Nutrient content of tree species of data from literature (a: g*kg^{-1} or b: % dry mass) was preferable analysed from leaves and twigs. The nutrient content was calculated by:

M_{Nu} (g/kg) * BRsp formula 1.4a or M_{Nu} (% of DM) * BRsp formula 1.4b

When P content was not known from literature, it was calculated by dividing the N content by 10 (mean N:P ratio from *Salix. cinerea* and *Carex* spp.)

C. Sedges

In order to make an estimation of the contribution of sedges, reed and grasses to the removal of nutrients by moose, of six sedge species (*C. elata* (n = 11), *C. appropinquata* (n = 8), *C. lasiocarpa* (n = 3), *C. nigra* (n = 3), *Carex acuta* (n = 1), *C. rostrata* (n = 1)), the N and P content (data pers. inf. Bormans M., 2010) were used. Per species the nutrient content was analysed with a sub-sample from a sample with a mixture of several individuals of the species. Every sample originated from a different site. Formula 1.4a was applied to calculate the nutrients removed from sedges.

D. Herbs

With a view to estimating the nutrient content of removed herbs by moose, five herbs (*Potentilla palustris* (n = 14), *Menyanthes trifoliata* (n = 10), *Thelypteris palustris* (n = 7), *Caltha palustris* (n = 5), *Equisetum fluviatile* (n = 4)) were used, as these are browsed by moose (microscopic and transect data). Formula 1.4a was applied to calculate the nutrients removed from herbs.

Results

1.1 Diet of moose in summer

1.1.1 Diet composition

The moose diet in summer in BNP consists for 48-87% of deciduous trees (which is trees and shrubs, Table 1.2), (Fig. 1.3 A B2). Grasses, sedges, reed and herbs represent together only maximum 1/5th (5-20%) of the total diet (Fig 7A, B2). Mosses form a very small part (2.1%) of the diet as well (Fig. 1.3 B1, B2). Of the microscopic data almost 40% ("veins" and "unknown", (Fig. 3 B1)) could not be assigned to an obvious category (Fig. X.79 and X.80). Concerning woody browse, 11% was only recognised as "twigs", though it could not be determined at species level (Table 1). Furthermore, 51-57% of the moose diet consists of *Salix* spp., of which at least 48-59% belongs to *Salix cinerea* (Table 1.2). *Betula* spp. represents 4-11% of the moose diet, of which 4-9% consist of *Betula pubescens*. Almost no conifers seem to be browsed during summer. Further on, conifers will be excluded, as they belong to winter browse (AppendixVII). Concerning herbs, (1-2%) and monocots (10-17%) (Fig. 1.3 B1, B2), the largest part was not attributable to one of the reference species. Furthermore 2-4% of the diet consisted of tall sedges (Table 1.2).

1.1.2 Diet selectivity of moose

Moose have a clear preference for deciduous shrubs (Fig. 1.5 A1 and A2). Herbs, grasses, sedges and reed seem to be avoided. From those, *Carex* species were very abundant on the transects, in comparison with deciduous trees (Fig. 1.5 B). Looking at *Salix* species, *S. repens* is avoided (§1.2.2), but transect data show that *Salix caprea*, *S. nigricans* and *S. triandra* seem to be preferred even more than *S. cinerea* (Fig. 1.5 C1). However, their occurrence is far less than the occurrence of *S. cinerea* (Fig. 1.5 B), making them quantitatively less important as a contribution to the moose diet (Fig. 1.5 B). *S. cinerea* was the most abundant of the tree species on the transects (Fig. 1.5 B). *Betula pubescens,* by contrast, is avoided as this species is not browsed that often compared with its occurrence (Fig. 1.5 B, C1, C2). The other birch species, however, *Betula pendula* and *B. humilis*, are preferred. *Frangula alnus* seems to be preferred according to transect data, but this does not correspond to the microscopic data. This species seems rather to contribute to the diet of roe deer (Table 1.5). Based on microscopic data, *Sorbus aucuparia* seems to be positively selected, but transect data do not correspond (Fig. 1.5 C1, C2). *Alnus glutinosa* is abundant (Fig. 1.5 B), but clearly avoided.

Diet composition in summer

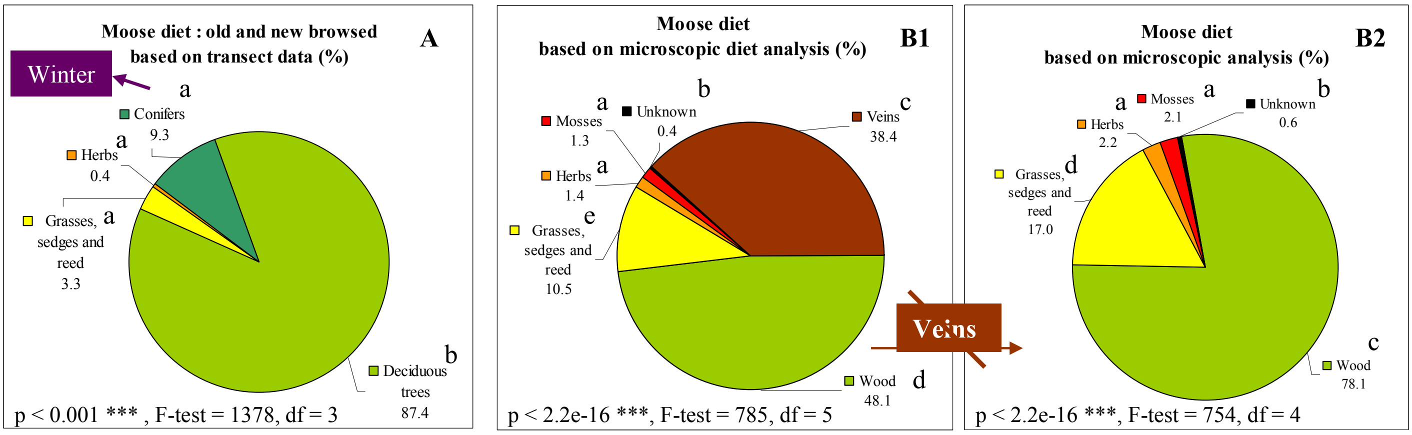


Fig. 1.3: Moose diet, proportions of means (based on weighed averages). A: Data from transecting, number of transects = 74, in total 6242m², conifers are clearly winter data, and the part of deciduous shrubs is overestimated, due to winter browsing as well, as shown by the microscopic data, the rest contributes to the summer diet. B1: Data from microscopic diet analysis of pellet samples, number of samples = 69. A1: Undefined: 38,4% veins, 0,37% undefined. B2: Veins are excluded, assuming they belong equally to all categories. Wood: 67.3% deciduous trees, 10.6% twigs, 0.02% conifers. Statistically significant differences ($p<0.05$) of frequencies between the categories are indicated by **different** letters.

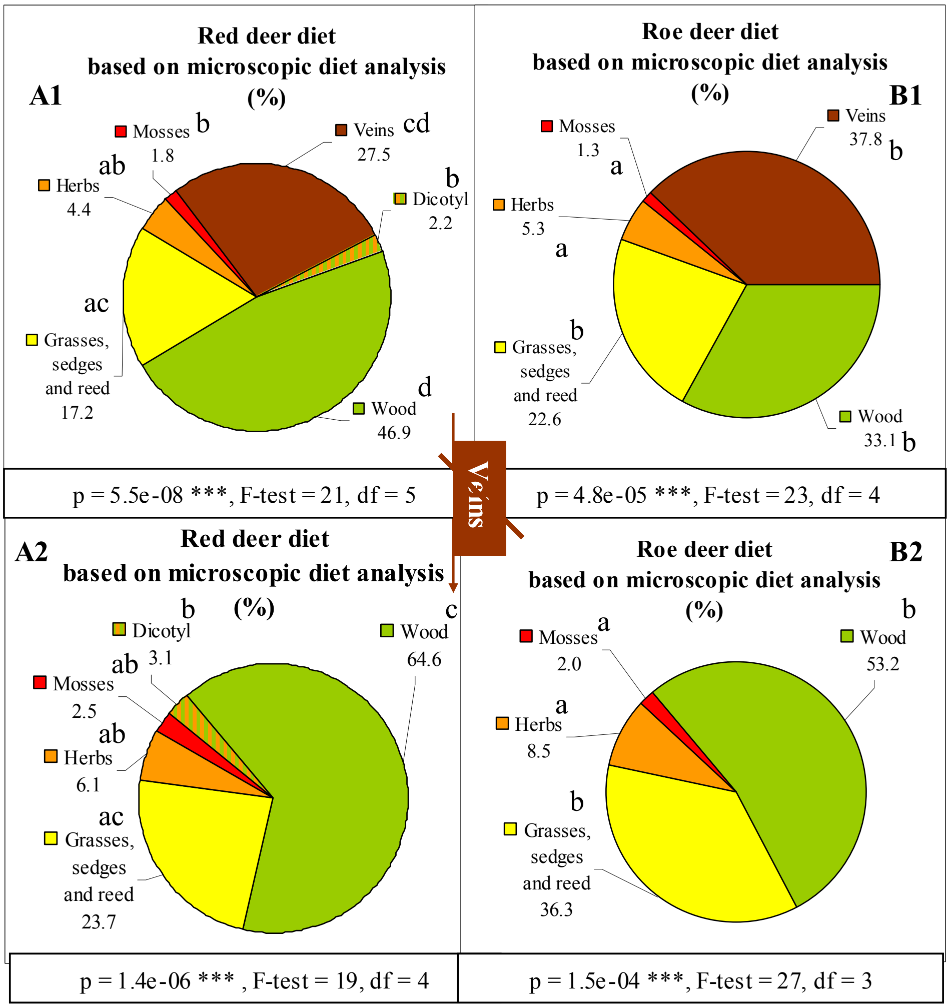


Fig. 1.4: Data from microscopic diet analysis of pellet samples. A1: Red deer diet (n = 5) proportions of means. B1: Roe deer diet (n = 5) proportions of means. In the diet of roe deer some seeds were found (μ = 0.25; sd = 0.50), but they are not shown in the graph. A2 and B2: Veins are excluded, assuming they belong equally to all categories. A2: Wood includes: deciduous trees: 54.7%, twigs: 10.3%, conifers: 0%. B2: Wood includes: deciduous trees: 50.03%, twigs: 3.0%, conifers: 0% "Unknown" was zero for red and roe deer, dicotyl was zero for roe deer. Statistically significant differences ($p<0.05$) of frequencies between the categories are indicated by **different** letters.

Table 1.2: Species contributing to the moose diet. A comparison of two methods: transect data and microscopic diet analysis.
For the microscopic data veins were excluded, assuming they belong equally to all categories. "n.a." means: not assessed. For microscopic data this means this species did not belong to the reference category and was as such not recognised as separate species (though it might be part of the larger "categories" that group some species as "twigs", "herbs" and "monocotyl". The latter is placed in the category "grasses, sedges and reed. Sample sizes: transect data: moose: n = 68, microscopic data: moose: n = 77; red deer: n = 5, roe deer: n = 3. Veins are excluded: Moose (38.4 ± 9.98)%; red deer (27.2 ± 6.0)%; roe deer (37.8±19.6)%.

Ungulate			Moose			Red deer		Roe deer	
Data source			Transect data	Microscopic data					
Plant category	Subdivision	Plant species	Proportion browsed (%)	Weighted average (%)	Sd	Weighted average (%)	Sd	Weighted average (%)	Sd
Wood	Deciduous shrubs	*Salix cinerea*	48.31	56.58	18.18	45.33	22.55	28.15	22.65
		Salix nigricans	1.94	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
		Salix pentandra	1.47	3.35	3.89	2.75	2.75	2.01	2.02
		Salix repens	0.53	0.31	0.97	0.27	0.61	0.80	1.61
		Salix triandra	0.16	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
		Salix caprea	0.14	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
		Betula pubescens	9.28	3.59	3.45	1.65	1.15	3.22	1.31
		Betula humilis	0.78	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
		Betula pendula	0.47	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
		Frangula alnus	20.39	0.90	1.63	1.92	4.30	5.23	4.23
		Populus tremula	1.51	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
		Sorbus aucuparia	0.46	1.16	1.57	2.20	1.23	2.41	2.08
		Corylus avellana	0.46	0.02	0.19	0.27	0.61	0.00	0.00
		Viburnum oplulus	0.42	0.17	0.49	0.55	0.75	1.61	1.31
		Quercus robur	0.38	0.45	1.00	0.55	0.75	2.41	2.08
		Alnus glutinosa	0.31	0.14	0.67	0.27	0.61	1.61	2.27
		Ribes nigrum	0.24	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
		Tilia platyphyllos	0.23	0.02	0.19	0.00	0.00	0.00	0.00
	Conifers	*Pinus sylvestris*	6.36	0.16	0.19	0.00	0.00	0.00	0.00
		Abies picea	3.06	0.00	0.00	0.00	0.00	0.00	0.00
	Undefined	Twigs	n.a.	10.53	10.24	7.97	9.74	5.90	7.29
Herbs	Undefined	Undefined herbs	0.05	1.18	1.13	3.02	4.05	7.24	2.08
		Equisetum fluviatile	0.00	0.64	1.76	0.00	0.00	0.40	0.80
		Menyanthes trifoliata	0.00	0.43	1.06	1.37	1.68	0.00	0.00
		Nuphar luteus	0.00	0.40	1.22	0.27	0.61	0.40	0.80
		Hydrocharis morsus-ranae	0.00	0.26	0.82	0.27	0.61	0.00	0.00
		Thelypteris palustris	0.00	0.12	0.42	0.55	1.23	0.00	0.00
		Eupatorium cannabinum	0.00	0.07	0.58	0.27	0.61	0.00	0.00
		Potentilla palustris	0.00	0.05	0.27	0.00	0.00	0.00	0.00
		Vaccinium myrtillus	0.29	0.00	0.00	0.27	0.61	0.00	0.00
		Ceratophyllaceae	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Caltha palustris	0.04	0.00	0.00	0.00	0.00	0.40	0.80
Dicotyl	Undefined		n.a.	n.a.	n.a.	3.02	6.76	0.00	0.00
Grasses, sedges and reed		Monocotyl	n.a.	8.38	7.81	9.89	8.55	17.69	13.60
		Tall Carex	2.30	3.78	4.89	6.32	6.91	5.63	2.79
		Typha latifolia	0.13	2.13	3.02	0.27	0.61	1.21	1.54
		Poaceae	n.a.	2.13	2.98	6.59	5.94	11.26	16.46
		Small Carex	0.00	0.31	0.85	0.82	1.84	0.40	0.80
		Juncus	0.00	0.05	0.27	0.00	0.00	0.40	0.80
		Phragmites australis	0.94	0.02	0.19	0.00	0.00	0.00	0.00
Mosses			0.00	2.10	2.21	3.30	6.90	1.61	3.22
Undefined		Undefined	0.00	0.59	1.07	0.00	0.00	0.00	0.00
		Veins	n.a.	excluded	excluded	excluded	excluded	excluded	excluded

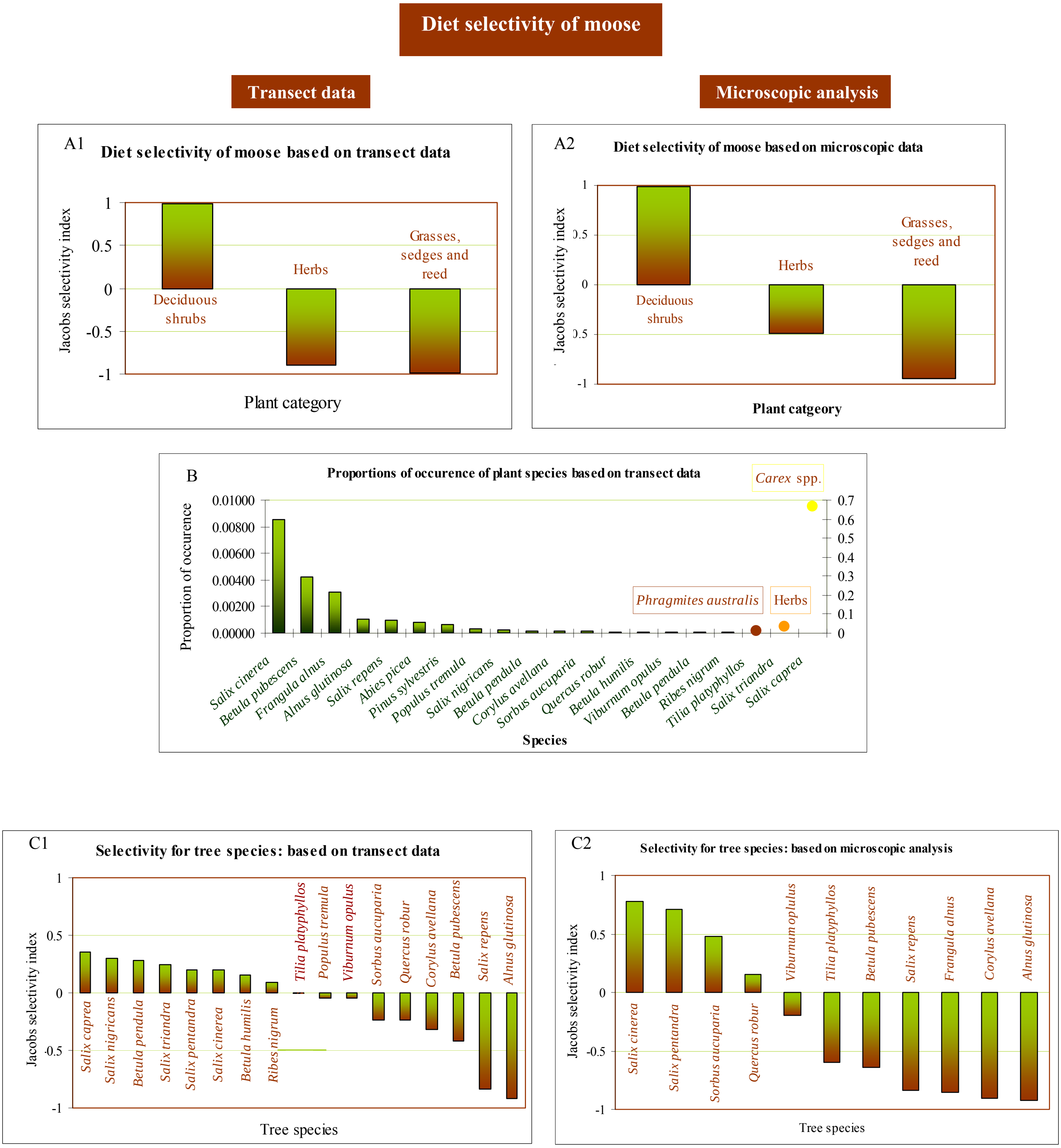


Fig. 1.5: Diet selectivity of moose, based on the Jacobs selectivity index: a value between -1 (negatively selected, avoided) and +1 (positively selected, preferred). Species, based on weighted averages. Sample sizes: number of transects = 74, in total 6242m²; microscopic data n = 77. B: Mean proportion per species occurring per transect. Occurrences of individuals of sedges, reed and herbs are estimated. C1 en C2: Selectivity for tree species based on transect data and microscopic analyses.
Conifers (*Abies picea* and *Pinus sylvestris)* (winter diet) was exluded in A and C and *Frangula alnus* (roe deer diet) was excluded in C1.

1.1.3 Comparison of the moose diet with other ungulate species

There is no significant difference between the diet of the ungulate species (p = 0.70, p = 0.13, p = 0.45; Table 1.3). Microscopic analysis of pellets, show a high percentage of deciduous trees in the diet of red and roe deer (Fig. 1.6; Fig. 1.4) and as such, this proportion is not significantly different from the proportion of deciduous trees in the diet of moose (p = 1.00, p = 0.26) (Fig. 1.6). Remarkably, no significant differences at all were found between the diet of red deer and moose. Nevertheless, roe deer have a significant larger part of "grasses, sedges and reed" than moose (p = 0.01; Table 1.4).

Table: 1.3: Comparison of the diet of ungulates: moose (n=77) (grey), red deer (n= 5) (brown), roe deer (n=4) (yellow). Based on microscopic data. Significance levels: ns: not significant; *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

Comarison of the ungulate species	Interaction		Differences between % browsed between			
	species - plant category		categories		species	
	p-value	F-test	p-value	F-test	p-value	F-test
Moose - Red deer	< 0.01 **	3.3	< 0.001 ***	800.1	0.70 ^{ns}	0.2
Moose - Roe deer	< 0.001 ***	2.3	< 0.001 ***	804.6	0.13 ^{ns}	5.7
Red deer - Roe deer	0.32 ^{ns}	1.2	< 0.001 ***	56.8	0.45 ^{ns}	0.6

Table 1.4: Comparison of the diet of ungulates. "Veins" is actually no plant category, and are assumed to belong equally to all categories. Significance levels: ns: not significant, *: p<0.05.

Differences in diet	Plant → categories	Deciduous shrubs (1)	Grasses, sedges and reed (2)	Herbs (3)	Mosses (4)	Conifers (5)	Veins (6)
Moose - Red deer	p-value	1 ^{ns}	0.51 ^{ns}	0.68 ^{ns}	1 ^{ns}	1 ^{ns}	0.17 ^{ns}
	difference (%)	0.6	-5	-5	7	8	7
Moose - Roe deer	p-value	0.26 ^{ns}	0.01 *	0.09 ^{ns}	1 ^{ns}	1 ^{ns}	1 ^{ns}
	difference (%)	7	-10	-8	0.8	0.08	0.4
Red deer - Roe deer	p-value	0.91 ^{ns}	0.99 ^{ns}	0.99 ^{ns}	1 ^{ns}	1 ^{ns}	0.92 ^{ns}
	difference (%)	7	-5	11	1	0	-6

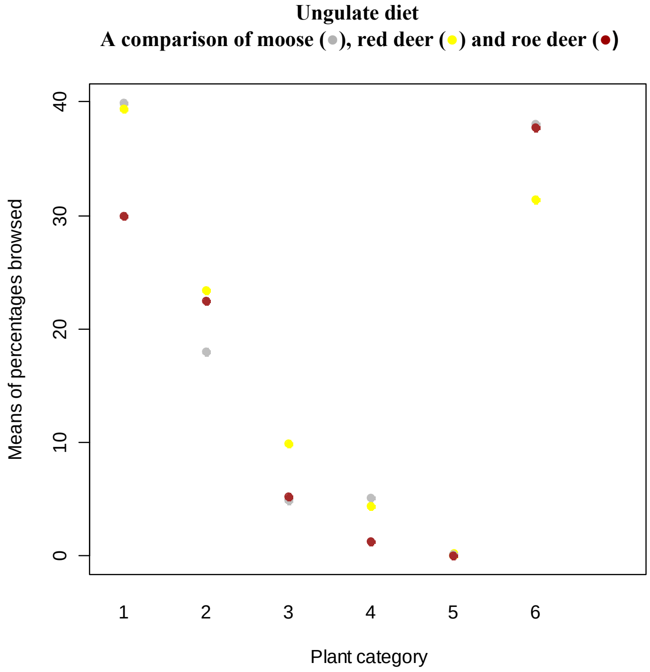


Fig. 1.6: Comparison of the diet of ungulates: moose (n=77) (grey), red deer (n= 5) (brown), roe deer (n=4) (yellow), based on microscopic data. Plant categories: 1 = deciduous trees; 2 = grasses, sedges and reed; 3 = herbs; 4 = mosses; 5 = conifers, 6 = veins. The latter is actually no plant category, it is assumed to belong equally to all categories. Based on microscopic data.

1.1.4 Comparison of methods

The two methods used to determine the diet of moose give very similar results (p = 0.78, F-test = 0.08, df =1) (Fig. 1.7). The *order of rank* of the contribution of plant categories to the diet is almost equal. A significant difference between the methods was only found considering the proportion of deciduous shrubs (p < 0.001**; Table 1.5). Furthermore, only small differences between the methods occurred. Grasses, sedges reed and herbs seem, as expected, to be slightly, though not significantly (p = 0.09; p = 0.95), underestimated in the field when comparing with the microscopic data. In both methods, there were differences between the *plant categories* in percentage browsed (p < 2.2e-16 ***, F-test = 199, df = 4).

A significant interaction between method and plant category was found (p = 8.3e-07 ***, F-test = 8.6, df = 4), yet this only indicates the methods do not always give the same result about the categories. This means that if a difference in browse percentage between categories occurs, it is not easy to conclude if this is caused by the method and/or by a real browse difference between the plant categories. Consequently, mosses were only detected by the microscopic method, as they were not considered when counting browse signs on transects. Next to this, conifers were only suggested to be part of the diet by the transect method. The first (mosses) is considered as a real difference between the categories, the second (conifers) as a difference caused by the method (further explained in the discussion, §1.1.3)

Table 1.5: Comparison of the methods, concerning plant categories: significance levels:
ns: not significant, **: p<0.01.

Plant categories	Deciduous shrubs (1)	Grasses, sedges and reed (2)	Herbs (3)	Mosses (4)	Conifers (5)
p-value	< 0.001 **	0.09 ns	0.95 ns	0.67 ns	0.98 ns
difference (%)	12	-8	-3	-5	3

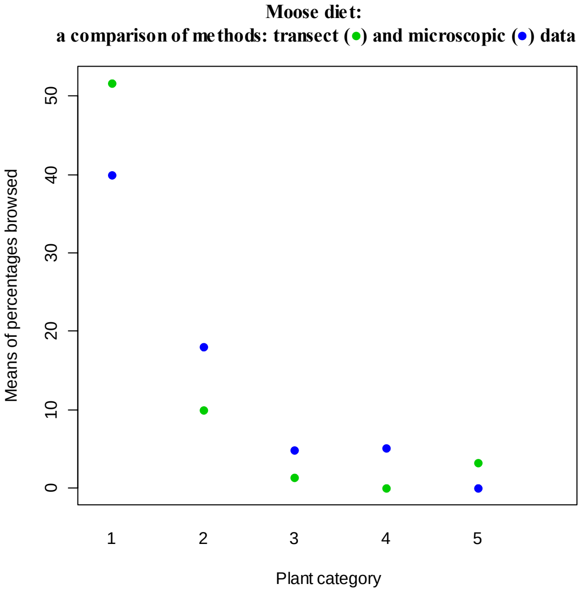


Fig. 1.7: Comparison of the methods: data of moose diet. Methods: green = transect data; blue = microscopic analysis data (veins, twigs and unknown data were excluded). Plant categories: 1 = deciduous trees; 2 = grasses, sedges and reed; 3 = herbs; 4 = mosses; 5 = conifers. The interaction plot shows largely similar results between the methods concerning plant categories.

1.1.5 Is there a link of browsing frequency with plant height and water level?

In general, a browse optimum for moose seems to be between 0.8m and 2m (Fig.1.9A). The percentage browsed is the highest in the driest places (Fig.1.9B), also indicated by the negative correlation between browsing and wetness (Fig.1.9). The biplot shows a positive correlation between plant height and plant species. A positive correlation is also found between wetness and structural vegetation type. Structural vegetation type is positively correlated with browsing too, suggesting that a certain structural vegetation type is preferred for browsing as shown in figure 1.10. Browsing and plant species are not very well correlated, suggesting that not always the same species was browsed (Table 1.3). Structural vegetation type and plant height are negatively correlated as well, meaning that a certain type is not linked with a certain plant height.

Preferences of moose for species may be linked to plant height and wetness. Of the preferred tree species, *Salix caprea* and *Salix cinerea* have an optimal height (IV.36). The percentage browsed, for both, is largest in dry places, though *Salix cinerea* occurs more frequently in somewhat wetter places (10 – 30cm). Of the avoided tree species *Alnus glutinosa*, only few are browsed on shrub height and most of the browsing occurred in wet areas (Fig.IV.37). Of *Alnus glutinosa* a lot of old trees occured, but of *Betula pubescens* a lot of young trees and of *Salix repens*, very small shrubs occurred on the transects.

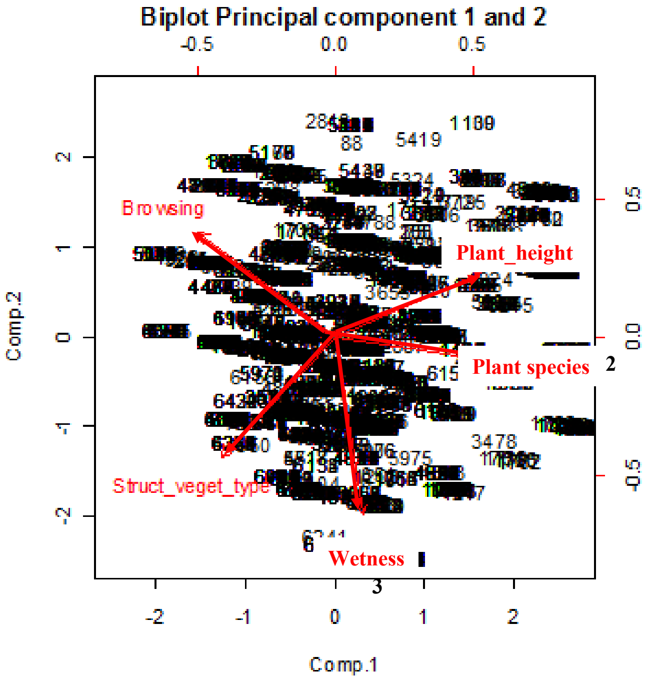


Fig. 1.8: The biplot shows the correlation between plant height (4 categories: < 0.8m; 0.8m - 2m; 2m - 5m; >5m); and plant species (Table 1.3); water level (4 categories: <10cm, 10cm - 30cm, 30cm - 50cm, >50cm); structural vegetation type (sedge marsh, reed marsh, brushwood, brookforest and coniferous forest) and browsing (browsed/unbrowsed). Data: over all transects, the numbers represent individual plants (total number: 6688). The First principal component expresses 32% and the second principal component 25% of the total variation.

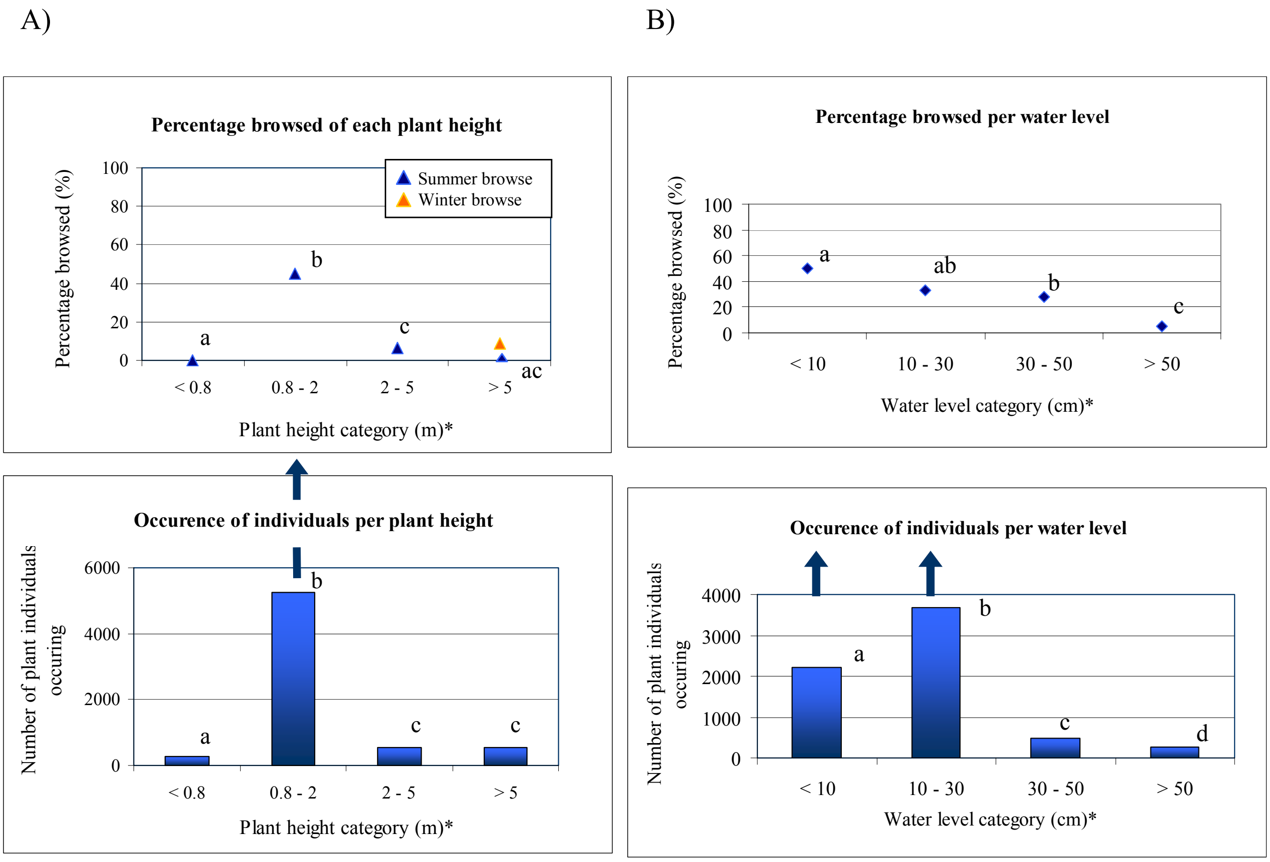


Fig. 1.9: A: Influence of plant height on browsing percentage. Categories: < 0.8m are mostly seedlings of trees and shrubs and small herbs, grasses and sedges (herb, grass sedge and reed seedlings were not taken into account); 0.8m – 2m are small trees and shrubs and most herbs and sedges; 2m - 5m are mostly young trees; > 6m are mostly old trees. ▲: indicates a slightly higher browsing percentage, when taking into account winter browsing on old *Abies picea* trees. It is possible to browse them on "moose height" because they still have low branches at an older age.
B) Influence of water level on browsing percentage.
"Number of plant individuals occurring" is the total number individuals of each category counted, summed over all transects. Numbers of browsed individuals are summed for all transects as well. The arrow shows the category with the highest percentage browsed.
"*" On the x-axes indicates that individual plants are assigned to categories by *estimating* their height and the water level at their location (always done by the same person).
Statistically significant differences ($p<0.05$) of frequencies between the categories are indicated by **different** letters.

1.2 Place of nutrient removal

There is no significant difference between the browsed percentages of the structural vegetation types (Fig. 1.10; p = 0.10, F = 2.5, df = 3, Table V.21). In all structural vegetation types the deciduous trees are significantly more browsed than grasses, sedges and reed and herbs, unless in the brook (Fig. 1.11 A; Tables V.22-V.27). *Salix cinerea* is the most abundant tree species in the brushwood type and 70% of those are browsed (Fig. 1.11 B2). Although, brushwood patches are scattered in the study area of BNP, the percentage browsed in a brushwood connected to the forest on one hand and brushwood islands in the open fen does not differ (Fig. 1.12, Appendix III Table …, p = 0.53, F-test = 0.40, df = 1).

Brook forests have a high browsing percentage as well (Fig. 1.11 B2). However, this is mainly due to *Frangula alnus*, frequently growing in these forests, which seemed to be more browsed by roe deer (Table 1.3). Browsing percentages in reed and sedge marsh are very low (Fig. 1.11 B4). Here as well, though, *Salix cinerea* is the most occurring tree species and the most browsed one. In the coniferous forest a high browsing percentage was found, yet due to winter forage. Therefore, it is not included in Fig. 1.14 (Appendix VII).

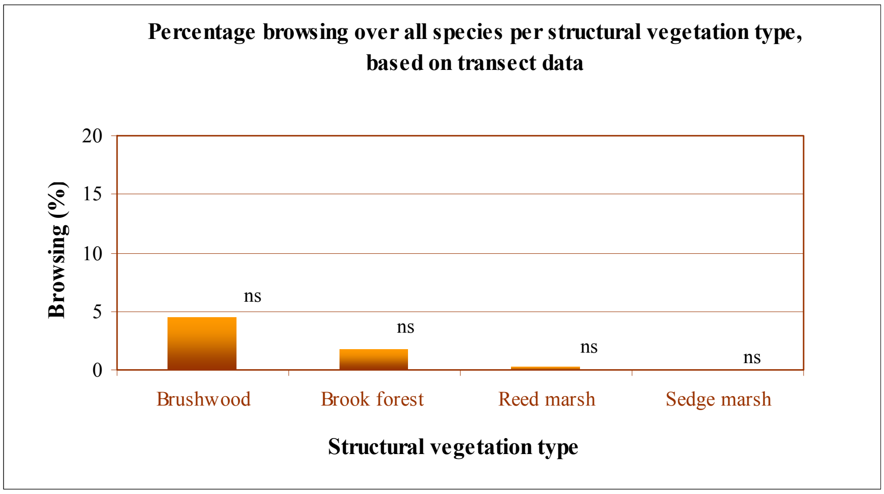


Fig. 1.10: Habitat use for browsing in summer. Percentage browsed (based on weighed averages), average percentage browsed with respect to the average percentage plants occurring. Over all species per structural vegetation type, based on transecting. Number of transects = 74, in total 6242m². Number of transects per type: brushwood: 31 (2656m²), brook forest: 19 (1276m²), reed marsh: 11 (546m²), sedge marsh: 11 (1177m²). Coniferous forest: 5 (547m²) is excluded as it is winter habitat for moose. Ns = not significant.

1.3 Amount of nutrients removed by moose

The amount of nutrients removed by moose is given in Table 1.6, more details on the results are given in Appendix III.

Table 1.6: Biomass intake (kg*ha^{-1}*yr^{-1}), calculated for three sites and their corresponding moose densities.

Site	Moose density moose*1000ha^{-1}	Biomass intake (kg*ha^{-1}*yr^{-1})	N removal (kg*ha^{-1}*yr^{-1})	P removal (kg*ha^{-1}*yr^{-1})
BNP	3	6	0.3	0.03
Outside the brushwood	10	21	1.1	1.12
Brushwood	30	64	3.2	0.32

Percentages browsed
of the proportion occurring
per structural vegetation type

A

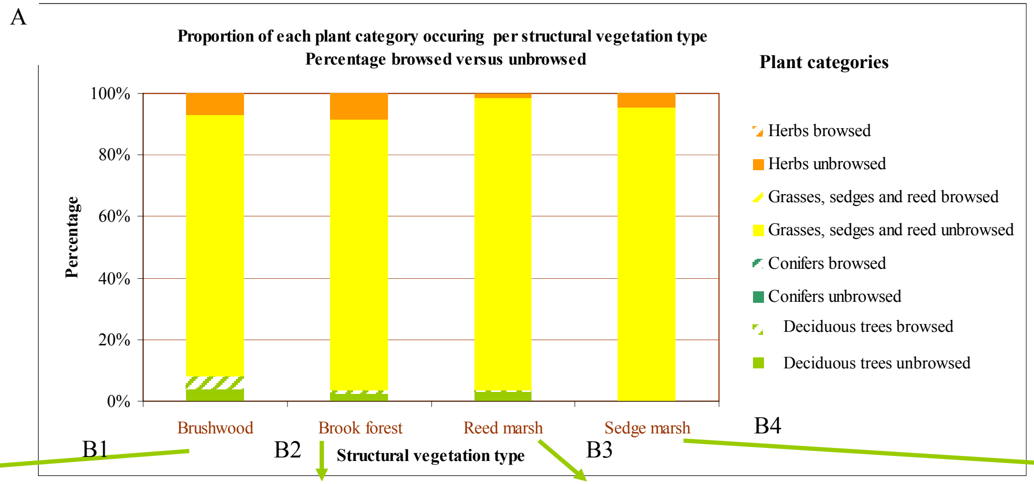
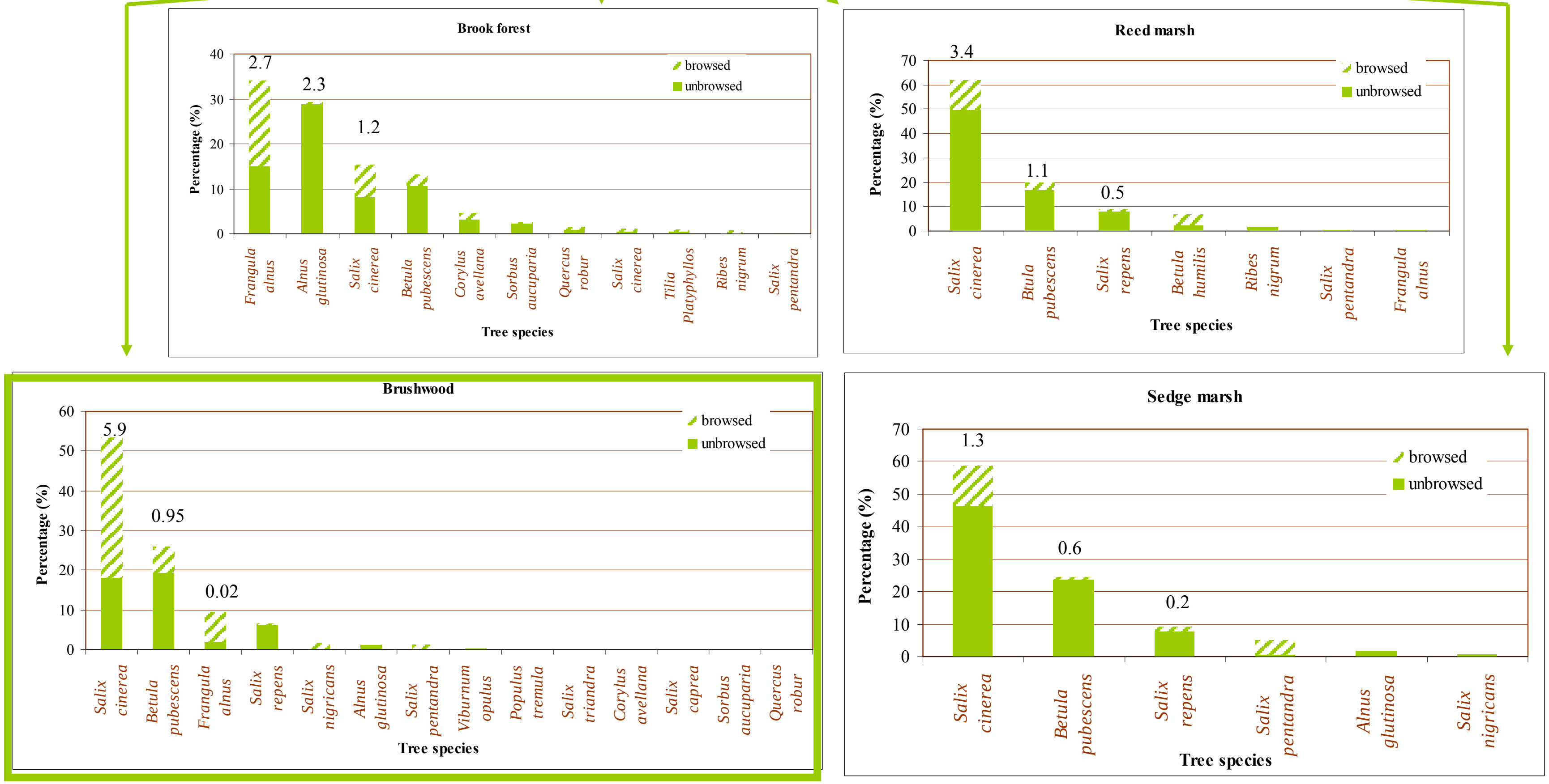


Fig. 1.11: A: Per structural vegetation type, the proportion of each plant category occurring per structural vegetation type was given. Percentages browsed of these were given as shaded. For the deciduous shrubs graphs per structural vegetation types were made (B1-B4).
The bars in total give the proportion (%) of each species occurring in the structural vegetation type. The shaded parts are the browsed percentages of the these totals. The number on top give the weighed mean number of individuals of the species occurring per transect.



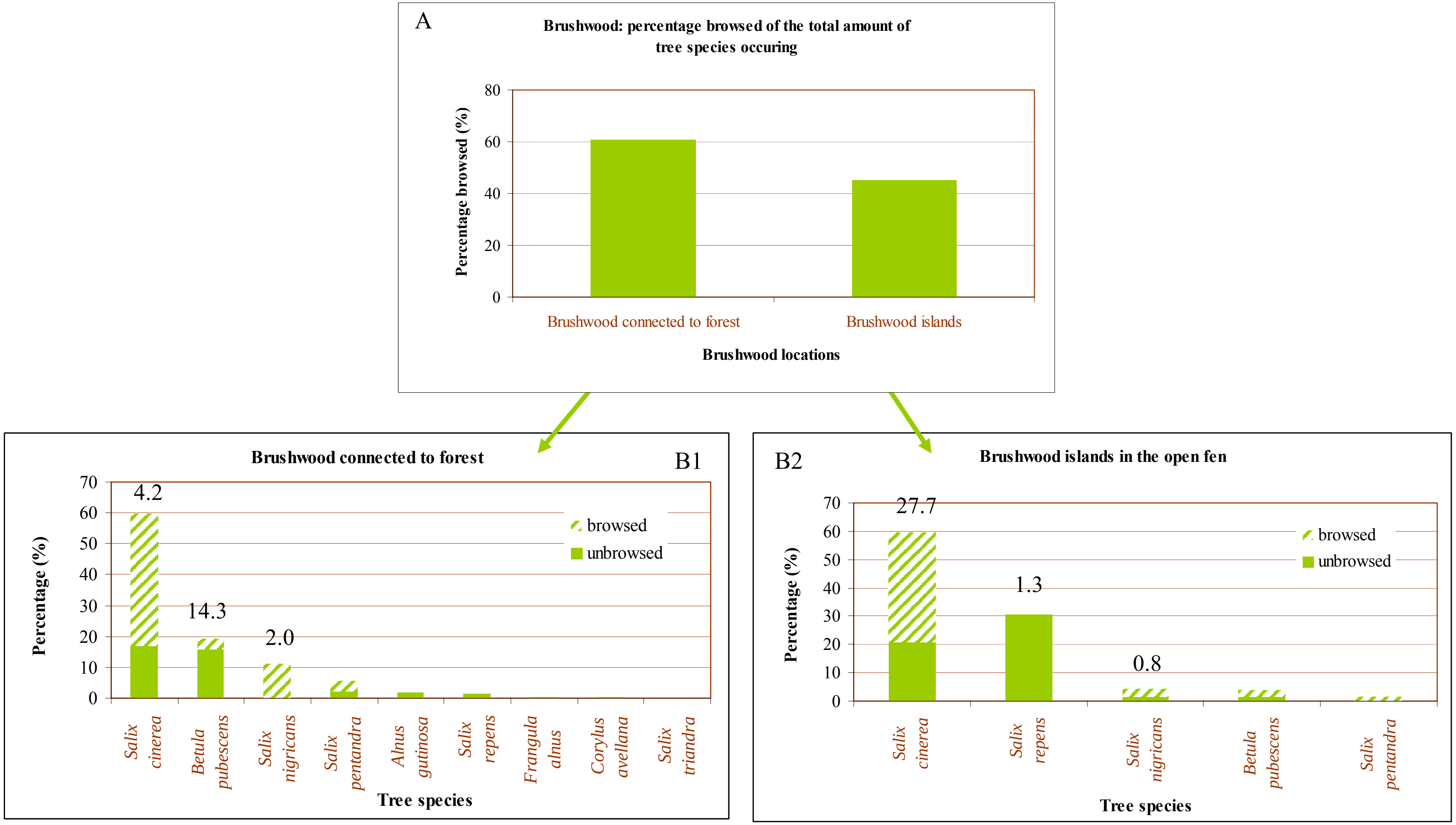


Fig. 1.12: This figure shows if there is no significant difference between the percentage browsed of brushwood connected to the forest side and brushwood islands in the open fen (p = 0.53, F-test = 0.40, df = 1).

DISCUSSION

1.1 Diet of moose in summer

1.1.1A Plant category proportions

The summer diet of moose in BNP is dominated by deciduous trees and shrubs, which is compatible with many regions (Zheleznov-Chukotsky & Votiashova, 1998; Appendix VI). A study in the Augustów forest, nearby BNP showed a similar contribution of trees and shrubs to the moose diet (Morow, 1976). In this study only August and September were considered to estimate the summer diet. However, food habits of moose depend strongly on *availabilities* and therefore may change monthly (Zheleznov-Chukotsky & Votiashova, 1998). In Russia, moose consume woody browse in spring, more herb species in summer and shrubs are main food in autumn (Zheleznov-Chukotsky & Votiashova, 1998). By contrast, Dungan & Wright (2005) found that moose rely less heavily on willow in spring and fall when available biomass and nutrients are lower in the Rocky mountain National Park (NP). Moose in Alaska browsed frequently on aquatic plants (MacCracken *et al.*, 1997; Morris, 2002). Also MacDonald & Barrett (1993) and Baskin & Danell (2003) indicated the importance of water plants for the moose diet. Ohlson and Staaland (2001) stress the importance of aquatic plants in some regions especially with respect to the intake of minerals. However, some aquatic plants were investigated in this study as well, but the contribution of these species (being part of the category herbs, Table 1.2) to the summer diet of moose was small. Zheleznov-Chukotsky & Votiashova (1998) reported that moose in Russia consume water plants from the bottom of pools in large groups until ice does prevent them.

1.1.1B Species contributing to the moose diet and diet selectivity

In BNP moose browse largely on *Salix* spp. in summer, which is similar to consumption patterns in north America (Shipley, 2010; Stumph & Wright, 2007) and in Russia (Zheleznov-Chukotsky & Votiashova, 1998), where late summer diet consists for 75-91% of *Salix* spp. Nonetheless, species contributing to the diet differ between ecosystem types and regions. Some species, *Betula* spp. and *Salix* spp., seem to contribute to the diet in many regions though (Appendix VI). Zheleznov-Chukotsky & Votiashova (1998) and Dobarro *et al.* (2010) state that moose have a various diet in summer, which corresponds to the findings of this study, albeit of several species only small quantities contribute to their diet. In the latter study, 98 plant species and 3 mushroom species (spring and winter) were found to contribute to their year round diet. Although availabilities of food supply are important to determine the bulk food of moose in every season (Zheleznov-Chukotsky & Votiashova, 1998), moose may have some *preferences*, which means they consequently pick out certain species. Begon *et al.* (2009) state that an animal has a food preference when “the proportion of that type in the animal’s diet is higher than its proportion in the animal’s environment”. Deciduous shrubs are preferred in BNP, probably as their twigs and leaves have a high protein and fat content (Zheleznov-Chukotsky & Votiashova, 1998). Specifically, *Salix* species are preferred, as it offers high quality woody browse (LeResche & Davis, 1973 in: Dungan and Wright, 2005). The preference for *Salix cinerea* is striking and indicates that *many* of these shrubs are browsed, unless their occurrence was the highest from all shrubs and trees on the transects. This contrasts with the other abundant tree species, *Betula pubescens*, which is not preferred by moose. Bryant & Kurporat (1980) made a review on the moose diet and concluded that, for most moose populations, willow is the preferred species and the most dominantly occurring species in their diet. They have collected data of several articles and came to the conclusion that, in general, the order of preferences is *Salix* spp. > *Populus* spp. > *Betula* spp. > *Pinus* spp. > *Abies* spp. > *Alnus* spp. = *Picea* spp.

Moreover, Dearing *et al.* (2000 in: Shipley, 2010) states that, when herbivores consume at least 60% from one plant genus, they may be called a specialist herbivore. Diets in north America and Sweden consist largely of one species or genus as well, the species being specific to location (Shipley, 2010). Next to this, diet selectivity of moose is demonstrated by several authors (Edenius, 1993; Bergström and Danell, 1995; De Jager *et al.*, 2009; Dobarro *et al.*, 2010). By contrast, moose seem to be less selective in other areas (Zheleznov-Chukotsky & Votiashova, 1998; Shipley, 2010). In this respect, moose may not in general be seen as a "specialist" or "generalist" herbivore (Begon *et al.*, 2009) as this is dependent on the location and the scale of the measurements (Shipley, 2010).

1.1.2 Comparison of the moose diet with other ungulate species

Large caution is needed when interpreting the results of red and roe deer samples, as sample size is insufficient to draw conclusions. They may only suggest, if the diet might largely overlap or differ from the moose diet.

A similar part of woody species was found in the diet of red deer in forest ecosystems (Dzięciołowski, 1967; Gębczyńska, 1980; MacDonald & Barrett, 1993), as was found in this study. The part of grasses suggested to be grazed by this study was higher than revealed by Gębczyńska (1980), was very similar to the findings of Dzięciołowski (1967); However, it was lower than found by Krojerová–Prokešová *et al.* (2010) in a sub-montane area and by Jayakody *et al.* (2011) in a forest system. The studies of both Dzięciołowski (1967) and Gębczyńska (1980) found that herbs were consumed more than suggested in this study. Supported by these studies, red deer seems to have a large diet overlap with moose. Hence, if part of the browse and graze signs on the transect data belonged to red deer, counted as if they were from moose, they will not have changed much the proportions of plant categories consumed by moose *itself*. The part of woody browse may nevertheless be enhanced by incorporating signs of red deer browsing. This corresponds with the fact that the results of the transect data did not differ much from microscopic data, indicating that transect data gave a good estimation of the moose diet.

Concerning roe deer, this study suggests that they consume a larger part of grasses, sedges and reed than moose. Yet, in forest ecosystems, roe deer consumed mostly herbs and few woody species (Gębczyńska, 1980; MacDonald & Barrett, 1993). It may be concluded that the diet overlap of roe deer and moose is smaller than that of red deer and moose. Cederlund & Nyström (1981) confirmed that moose's capacity to digest plant species is higher than roe deer's capacity, due to an adaptation to woody forage of moose. Signs of roe deer browsing may thus become clear when transect data show a contribution of a plant species, meant to be browsed by moose, whilst microscopic data on moose's diet does not (results §1.1.3).

1.1.3 Comparison of methods

Data from transects and those from microscopic diet analysis show largely the same results, though both methods have their advantages and disadvantages. A weakness of the transect method is that browsing signs of other ungulates (red and roe deer) are partly included in the transect data, probably enhancing the wood part in the diet. Next to this, this method has slightly underestimated the grass, sedge and reed proportion as these are less easily noticed as being browsed than larger and less numerous species. Besides, transect data includes partly old signs of browsing, belonging to the diet of another season. As a consequence, conifers and woody species in general are overestimated, as they are browsed in winter (Appendix VII), clearly showed by their nearly absence in the microscopic data.

Yet, in contrast to the microscopic data, transect data give a more extended list of species browsed and besides, these may be determined with a higher certainty than in the microscopic diet. However, it has to be added that broadleaved willow species are not easily determined on species level and besides, some species hybridize causing a lot of transition forms with different morphological treats (De Fré & Hoffman, 2004). In addition, this method gives the opportunity to count the number of occurring species, making it possible to estimate if moose are selective.

A weakness of the microscopic data is that proportions of species that are very well digested may be underestimated as well, as they are not recognisable in the pellets anymore. Moreover, plants are only recognisable when they are included in a reference collection. Next to this, the reference collection made, was only based on leaves, of which the upper and back side, were not taken into account separately. However, between those, differences in cell appearances may occur (pers. inf. Emilia Hofman, 2010). Stems were not sampled either, however, species may be confused when looking at cells of the stem epidermis as they are commonly elongated and rather difficult to assign to the right species (pers. inf. Emilia Hofman, 2010). I trained myself to recognise plant fragments, though a specialist would probably get more out of the data. As I was not able to assign the veins to a correct category, 40% of the total diet of the microscopic data strictly remains unknown. Consequently, the microscopic data has to be considered with caution. Veins are probably abundant as browse digestibility is usually below 50% (Staaland *et al.*, 1992) (Appendix table III.18).

Yet, in contrast to the transect data, microscopic data take *specifically* the moose diet in consideration and assess with certainty only the *recent* diet composition, evidently when fresh pellets are collected. An unexpected plant category, mosses, contributing to the diet was not detected by transect data. Mosses are probably only eaten together with other plants as only trace amounts occur in their diet. Furthermore, monocotyledons and dicotyledons are easily distinguished from each other, causing a high certainty to put plant fragments in categories.

Dungan & Wright (2005) used observational data, collected by recording moose feeding behaviour in the field and data from microscopic analysis of pellets to assess the diet of moose in the Rocky Mountain NP. Their results were very similar to this study. Observational data underestimated the sedges and slightly overestimated the woody browse in comparison to the microscopic analysis.

To conclude, a combination of both methods might offer the possibility to correct for the weaknesses of both methods. Microscopic data has to be used, rather than the transect data, to consider the *proportion* of plant categories and the proportion of species, contributing to the moose diet. Transect data might be more precise to use considering which *species* are browsed and occurring.

1.1.4 Is there a link of browsing frequency with plant height and water level?

For moose, food availability and consumption depend on tree height (Bergström & Guillet, 2002). According to Bergström & Guillet (2002) bark and leaf stripping was done by moose until a maximum height of 2.5m. This maximum corresponds to the findings of this study, though moose seem to avoid "uncomfortable" low species as well. Moose prefer plant species at "moose height", which are mostly shrubs, but it is not clear if this is consequence or cause of browsing, or both. Considering *Salix cinerea,* the main browsed species, a circle movement may be going on. Because moose browse on shrubs, these are not able to develop to large trees on one hand, suggesting a growth suppression (Abaturov & Smirnov, 2002; Persson *et al.*, 2003b; Dungan & Wright, 2005). On the other hand, however, *Salix cinerea* makes multiple shoots at a low height (Werpachowski, 2007), "presenting" a lot of forage to moose. A strategy to escape from browsing, may be evolving to a tree form. This is clearly not the strategy of *Salix cinerea,* though.

Moose seem to prefer browsing on drier places during summer. The hypothesis may be stated that moose may avoid wet places with stagnating water, associated with many insects. Zheleznov-Chukotsky & Votiashova (1998), state that moose forage in riverine habitats, to avoid windless places with a lot of insects. Besides, Van Assche (2001a) states that moose spend a lot of time in and under water in summer to avoid insects.

To conclude, this means that biomass is preferably removed at places with a higher decomposition rate (Van der Linden *et al.*, 1996). Concerning brushwood, higher "silted islands" in the fen exists, which seemed to be favoured by moose.

1.2. Place nutrient removal

Fedyk *et al.* (1984) and Gebczyńska & Raczyński (1984) state that moose forage in willow and birch stands in BNP. The latter authors state that sedgy fenland is used too, in contrast to the findings of the former authors. Similar to the findings of Dungan & Wright (2005), stating that willow patches are the most commonly selected habitat by moose to forage, this study shows that in summer moose browse wherever *Salix cinerea* species occur. The fact that there is no significant browse difference between brushwood patches on different locations, supports this reasoning as well. MacArthur & Pianka (1966) state that the optimal utilization of time and energy comprises that "an activity should be enlarged as long as the gain in time spent per unit food exceeds the loss". Evidently, in brushwood, shrubs may be browsed more as a higher supply is available, though, this was not significantly proven in this study. It may be concluded, supported by other studies in BNP (Fedyk *et al.*, 1984; Gebczyńska & Raczyński, 1984) that browsing occurs mainly in brushwood *patches*, be it large patches, so-called brushwood, are be it small patches, so-called "islands". Brook forest seems to be used to forage as well, though concerning browse percentages, these were three times lower than those in brushwood. However, the fact that *Frangula* *alnus*, occurring abundantly as understory of brook forest, was the main browsed species, it may be suggested that brook forest is rather used by roe deer than by moose, to forage.

1.3 Amount of nutrients removed by moose

Although quantity and quality of browse vary between regions, there seem to be no significant differences between the daily intake rates of gross dry matter between regions (Saether & Andersen, 1989 in: Persson *et al*., 2000). The general moose density calculated over BNP is similar to those (3.1 - 5.0 moose/1000ha) estimated in 1983 in BNP with a number of 620 moose in BNP (Gebczyńska & Raczyński, 1983 in: Borkowska & Konopko, 1994) (Table III.17). In Białowieza forest the red deer density is 6/100ha (pers. inf. Kuijper, 2011), which may be compared with the moose density used for the areas other than brushwood. This indicates a rather low, though not irrealistic value of 1 moose/100ha in areas else than brushwood in BNP. The density used in the brushwood, is a very high density as Abaturov & Smirnov (2002) state that a density of 3-5 moose/1000ha is high. In comparison to the biomass intake by moose in BNP, around 20 to 40 kg*ha^{-1}*yr^{-1} was estimated to be removed in a study of Pastor *et al*., (1998) at Isle Royale NP with a moose density of around 180 moose/ha (which is very high) (De Jager & Pastor, 2009) (Table III.17).

Samples for nutrient analysis were only collected in June, nutrient content of other months was not analysed, though content may be lower in autumn and slightly higher in spring (Dungan & Wright, 2005). Therefore data of June may be seen as a “mean”.

CONCLUSION

Summer diet consists mainly of deciduous shrubs, of which 48-57% of the browsed species is *Salix cinerea*. The latter is preferred, in contrast to *Betula pubescens*, which is also abundant in the field. Supported by other studies in BNP, it may be concluded that browsing occurs mainly in brushwood *patches*, be it large patches, so-called brushwood, or be it small patches, so-called “islands”. Moose prefer to browse on shrub height and on dry spots, implying a higher decomposition rate.

PART 2: INPUT OF NUTRIENTS BY MOOSE

Introduction

The main aim of this part is to investigate the *amount* of nutrients, put in the ecosystem by moose. Firstly though, it is examined *where* moose cause a nutrient input. Specifically, pellet densities per structural vegetation type are investigated. Subsequently, pellets were counted on transects in different structural vegetation types (§2.1.1A) and in plots (§2.1.1B). The hypothesis states that the deposition occurs around rest places (Bokdam, 2001; Mouissie *et al.*, 2005). Therefore, it is examined in which vegetation type(s) rest places occur (§2.1.2). Finally, the amount of N and P deposited is calculated (§2.3). Firstly, nutrient concentrations are analysed from pellet samples (§2.3.1). Besides, few samples of red and roe deer are analysed to compare the amounts of nutrients with moose's samples. Secondly N and P concentrations in urine were are estimated using data from literature (§2.3.2).

Method

2.1 Place of nutrient input by moose

2.1.1 Pellet density per structural vegetation type

2.1.1A Transect data

Pellet heaps were counted on transects, in all structural vegetation types (details §1.1.A) (Fig. I.28), which is a frequently used method to assess pellet density (Borowski & Ukalska, 2008; Kuijper & Bakker, 2008). Only fresh pellets were used to make an estimation of pellet density per time, as these could be attributed to a defined time period (a month) (Månsson *et al.* 2011). "Fresh" pellet heaps are green, very soft and humid, "old" pellet heaps are not squeezable, have no gloss, are fragile inside and are not humid (Fig. II.32 and II.33)(Brown *et al*., 2009). The mean number of pellet heaps per hectare was calculated for fresh (Fig. 2.15 A) pellets. A weigh factor was applied (as in §1.1.A) as transects were not equally long. Data were square root transformed as they followed a Poisson distribution (Zar, 1999). Furthermore, a one-way ANOVA was used with Tukey (HSD) to look at differences in pellet densities (dependent variable) between structural vegetation types (independent variable) (Fig. 2.15).

2.1.1B Plot data

Yet, as pellet countings on transects seemed to be not so efficient, in view of the fact that pellets were rather clustered in patches than on straight lines, pellets were counted in plots as well. For further investigation, paired plots were created (Fig. 2.13), investigating always one brushwood type (n = 10) and one of the other structural vegetation types (n = 10), the latter depending on what was available. Other structural vegetation types included sedge marsh (n = 5), reed marsh (n = 4) and brook forest (n = 1). In the plots, number of pellet heaps and when possible number of pellets per pellet heap were counted. Each plot was 100m² (10m x 10m) and was recalculated per hectare. The data was collected between 27th of June and 1 July 2011. The fresh pellet density of one week, was counted and extrapolated to one month. A paired non-parametric Wilcox signed rank test was performed, as data were not normally distributed.

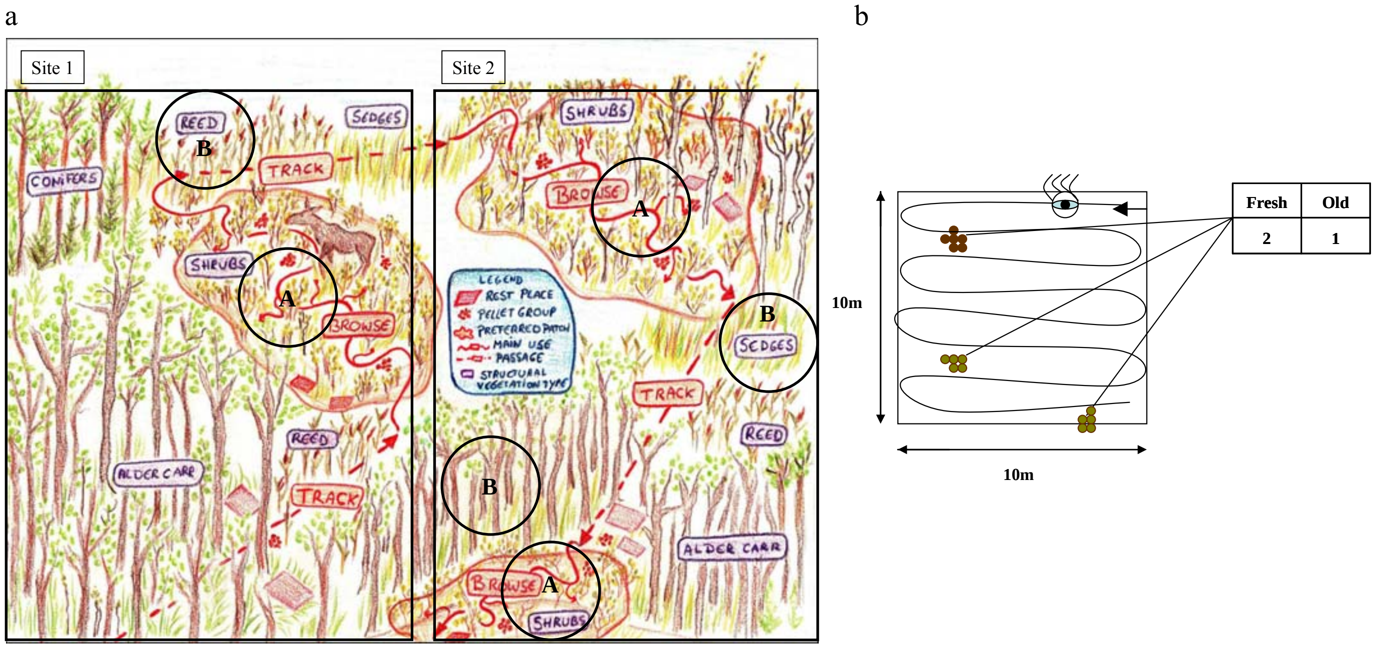


Fig. 2.13: a: Design of the plots. Paired measurements were created with one brushwood plot (A) and 1 of the other structural vegetation types (B) (brook forest, reed marsh or sedge marsh). b: In plots of 100m², pellet heaps were searched and counted.

2.1.2 Link of pellet deposition with moose paths and rest places

The number of moose paths and rest places were counted on the transects per structural vegetation type. Moose paths are typically very broad (Brown *et al.*, 2009) (Fig. 2.14) and recognisable as sedges, herbs and shrubs are trampled in a rough way. Moose's rest places look like rectangular combs in sedges (Fig. 2.14). Mean numbers of paths and rest places were calculated using a weigh factor (§1.1.A) for different areas of transects (Fig. 2.16). Data were square root transformed as they were Poisson distributed (Zar, 1999). To analyse the differences of numbers per structural vegetation type one-way ANOVAs and Tukey HSD were used. Besides the methods used, I recorded rest places and fresh pellets too when stumbled upon in the field.

Fig. 2.14: Left: moose path, right: two rest places of moose.

2.2 Amount of nutrients deposited by moose

2.2.1 Amount of nutrients in moose pellets

Chemical analysis was performed, using collected pellet samples (§ method 1.1.1B) and were carried out according to Walinga *et al.* (1989) with a SKALAR*, SAN ^{plus} SYSTEM. Although, on a part of the pellets fungi had been growing, for nutrient analysis, this did not matter as the nutrients were then part of the fungi, which were part of the sample. Mean and standard deviation of nutrient content of pellet samples over all individuals was calculated for moose, red and roe deer (Table 2.17). Data were normally distributed. To test for differences in nutrients between the ungulate species, a MANOVA was done, using the Pillai test. One-way ANOVAs and Tukey HSD tests were conducted for each nutritional element between the ungulate species (Table 2.8). A biplot was made based on a principal component analysis (PCA), to show correlations between amounts of macrocutrients over all species (Fig. 2.8).

2.2.2 Amount of pellets

Number of pellets per pellet heap was calculated using two datasets, one of summer (n = 6) and one of spring pellets (n = 11). The latter pellets were counted in April of 2011. This was only possible as few fresh pellet heaps pellets could be counted, because many of were diarrhoea (Fig. 2.17). Countings of winter pellets (in the coniferous forest) were not used, since the number of pellets per pellet heap seemed to be twice as high as those from summer and winter ($\mu = 80$, sd = 45, pellets of 50 old pellet heaps were counted).

2.3 Amount of nutrient input

2.3.1 Pellet deposition

The amount of nutrients (N and P) deposited per hectare was calculated using the pellet density of the *plot* data (Table 2.9). Amount of nutrients ($kg*ha^{-1}*yr^{-1}$) deposited by pellets is calculated:

$$\text{Pellet density } (\text{number}*ha^{-1}*yr^{-1}) * M_{drypellet}\ (g) * \text{Number}_{pelletsperheap} * \text{Nu content } (g*ha^{-1}) \quad \text{formula 2.5}$$

$M_{drypellet}$ (g) is the dry mass of a pellet (g); $\text{Number}_{pelletsperheap}$ is the number of pellets per heap; Nu content ($g*kg^{-1}$) is the nutrient (N or P) content ($g*kg^{-1}$).

Based on *transect* data, the input of nutrients by pellets in brook forest was calculated as 1/3rd of the input in brushwood.

2.3.2 Urine deposition

Since no data were collected considering urine deposition, therefore data from literature were used. Though, Persson *et al.* (2003) states that average values of dung and urine deposited turn out to be remarkably similar in different parts of the world. Belkovsky & Jordan (1981) measured that moose urinate $13.1L*day^{-1}$ in summer, containing $5.15gN*L^{-1}$ (Persson, 2000). Moose densities used are the same as calculated in §1.3.

The amount of N ($kg*ha^{-1}*yr^{-1}$) deposited through urine of moose in the growth season (7 months) can be calculated as follows:

Amount of urine ($l*day^{-1}*moose^{-1}$) * N content ($g*l^{-1}$)* 214days (7 months) * Number of moose*ha^{-1} formula 2.6

Since no data on P concentrations in urine of moose or deer were found, N/P ratios of other ruminants were used. As Kaneko *et al.* (2008) found a N/P ratio of around 10 in the urine of sheep and goat, this value was used to calculate the P concentration for moose by multiplying the N concentration with 0.10. This resulted in a concentration of $0.52gP*L^{-1}$. The amount of P by urine of moose deposited per hectare per year can be calculated as follows:

Amount of urine ($L*day^{-1}*moose^{-1}$) * (N content ($g*L^{-1}$) * 0.1) * 214days (7 months) * Number of moose*ha^{-1} formula 2.7

Results

2.1 Place of nutrient input by moose

2.1.1 Pellet densities

On the transects, fresh pellets were only found in brushwood (μ = 37, sd = 100 pellet heaps*ha^{-1}*$month^{-1}$) and brook forest (μ =11 sd = 49 pellet heaps*ha^{-1}*$month^{-1}$) in summer (Fig. 2.15 A). Yet, the differences in mean pellet heap densities between the structural vegetation types were not significant (p = 0.22, F = 1.5, df = 4). In the paired plots more than double as much pellets were found in the brushwood than elsewhere (brushwood: μ = 200 sd = 270 pellet heaps*ha^{-1}*$month^{-1}$; outside the brushwood type: μ = 86 (sd =170) pellet heaps*ha^{-1}*$month^{-1}$), but the difference was not significant (p = 0.24, V = 21)(Fig. 2.16). Nevertheless, observational data may support a trend suggesting that the pellet density is the highest in the brushwood (Appendix I, Fig. I.31). Besides, by collecting moose pellets for nutrient analysis (§ 2.2.1) and microscopic diet analysis (§1.1.1.B), I found many fresh pellets in the brushwood (willow) areas. On edges of brook forests few pellet heaps were found too (Fig. I.31).

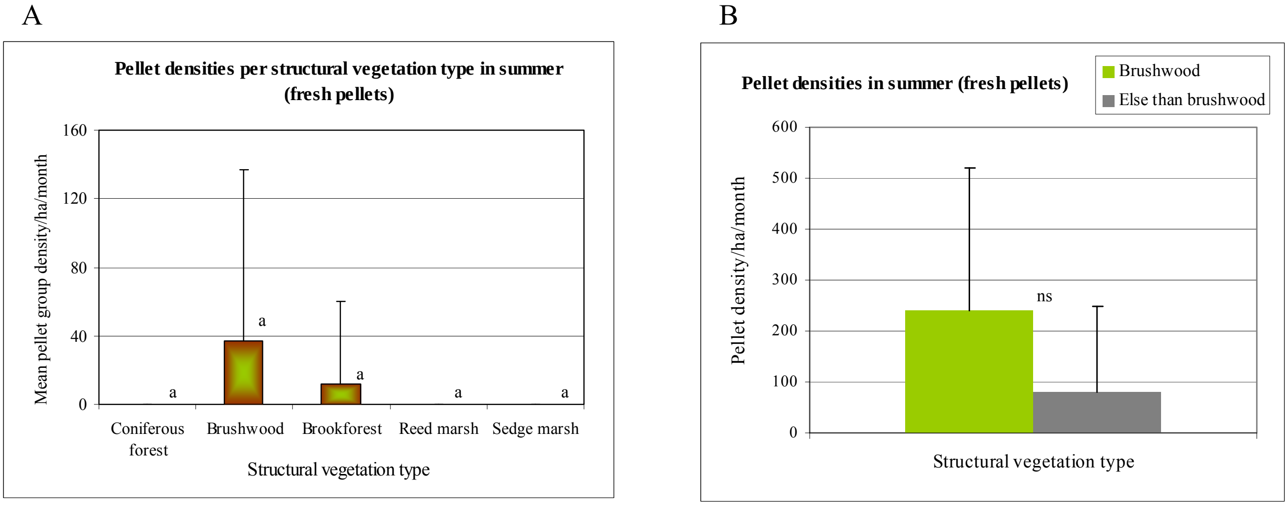


Fig. 2.15: A: Pellet densities in counted on transects (mean ± SE) (based on transect data, total number of transects = 74, in total 6242m²). Concerning the fresh pellets: moose pellets of one month were gathered Statistically significant differences (p<0.05) of frequencies between the categories are indicated by **different** letters. B: Pellet density counted in plots, (sample period was 1 week, extrapolated to one month) in summer (mean ± sd): paired plots of brushwood (n = 10) and else than brushwood (n = 10). Structural vegetation types else than brushwood were sedge marsh (5), reed marsh (n = 4) and brook forest (n = 1). Ns = not significant.

2.1.2 Link of pellet deposition with moose paths and rest places

Although numbers are slightly higher in the brushwood, no significant differences are found between structural vegetation types in moose paths and rest places (Fig. 2.16). Looking at the distribution of rest places and pellets found in the field, on transects, plots and during extra observations in the field, pellet heaps and rest places seem to be clustered, mainly in the brushwood (Fig. I.31). This map shows that rest places occur on edges of alder carr as well, along with pellet heaps. Concerning coniferous forest, rest places and paths could not be noticed, as low and weak vegetation (like sedges) is lacking in this type.

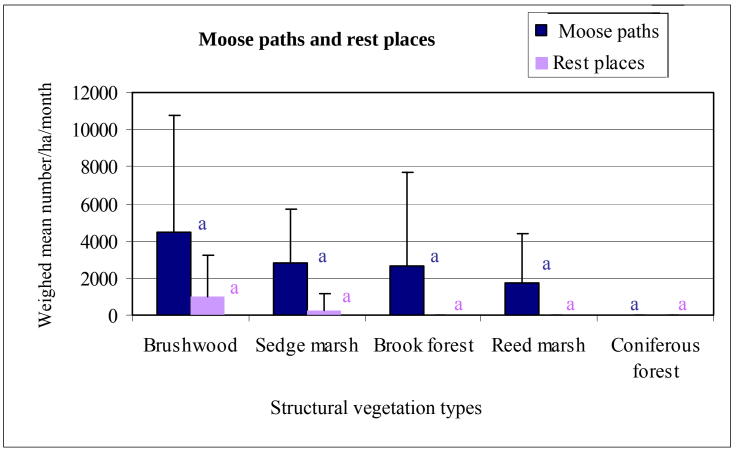


Fig. 2.16: Moose paths and rest places, mean and standard deviation. Statistically significant differences ($p<0.05$) of frequencies between the categories are indicated by **different** letters.

2.2 Amount of nutrient input

2.2.1 Nutrient concentrations in moose and ungulate pellets

The amount of nutrients deposited by moose is shown in Table 2.7. Besides, Fig. 2.7 shows there is a low variation in nutrient content in pellets (Fig. 2.7). A comparison of the amount of nutrients deposited by moose with those of the other ungulates, needs to be treated with caution, as more data of red and roe deer are needed to be able to draw conclusions. Roe deer seem to deposit significant larger amounts of N and P (Table 2.8) (Fig. 2.17) through pellets than red deer but not significant more than moose. The mean N content of moose is only 3/4th of the content of what red deer excrete through their pellets (Table 2.8). There is a good correlation between nutrient contents of the individuals (Fig. 2.18). There is a significant difference concerning the amount of nutrients between the three species (p = 1.609e-07 ***, Pillai test = 0.5222)(Table 2.8).

Table 2.7: Nutrient content of pellets (*Alces alces* (moose), *Cervus elaphus* (red deer) and *Capreolus capreolus* (roe deer)) Parameters: μ = mean and sd = standard deviation. In **bold**: most relevant values for this study.

Species	Sample size	Parameter	N $g*kg^{-1}$	P $g*kg^{-1}$	K $g*kg^{-1}$	Ca $g*kg^{-1}$	Mg $g*kg^{-1}$	Na $g*kg^{-1}$
Alces alces	68	μ	**24**	**3**	4	18	3	0.3
		sd	**3**	**0.9**	2	4	1	0.3
Cervus elaphus	5	μ	26	6	3	24	4	0.7
		sd	5	4	2	5	2	0.7
Capreolus capreolus	4	μ	33	8	4	31	7	0.6
		sd	5	4	4	5	2	0.2

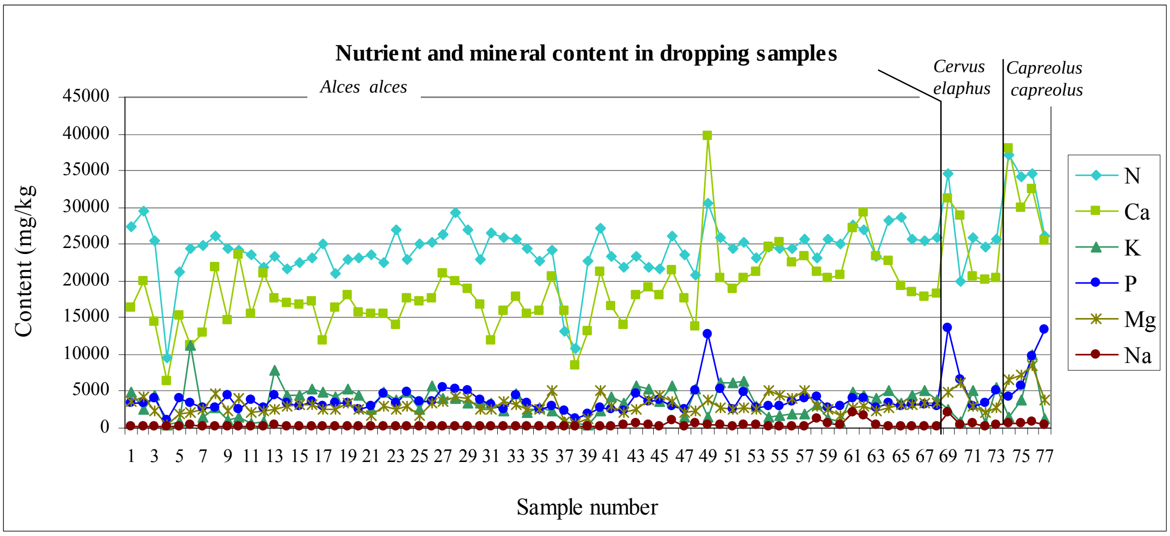


Fig. 2.17: Concentrations of macronutrients per dry mass per individual sample of pellets of *Alces alces* (n = 68), *Cervus elaphus* (n = 5) and *Capreolus capreolus* (n = 4).

Table 2.8: Differences of mean nutrient content (mg/kg) of pellets. Dropping sample size: *Alces alces* (n = 68), *Cervus elaphus* (n = 5) and *Capreolus capreolus* (n = 4). Significance codes: ns = not significant, “***” 0.001 “**” 0.01 “*” 0.05.

Species	N g*kg^{-1}	P g*kg^{-1}	K g*kg^{-1}	Ca g*kg^{-1}	Mg g*kg^{-1}	Na g*kg^{-1}
Alces alces - Cervus elaphus	- 2 ^{ns}	- 3 **	0.6 ^{ns}	- 6 *	- 0.9 ^{ns}	- 0.4 ^{ns}
Alces alces - Capreolus capreolus	- 9 ***	- 5 ***	- 0.6 ^{ns}	- 13 ***	- 4 ***	- 0.3 ^{ns}
Cervus elaphus - Capreolus capreolus	- 7 *	- 2 ^{ns}	- 1 ^{ns}	- 7 ^{ns}	- 3 **	0.1 ^{ns}

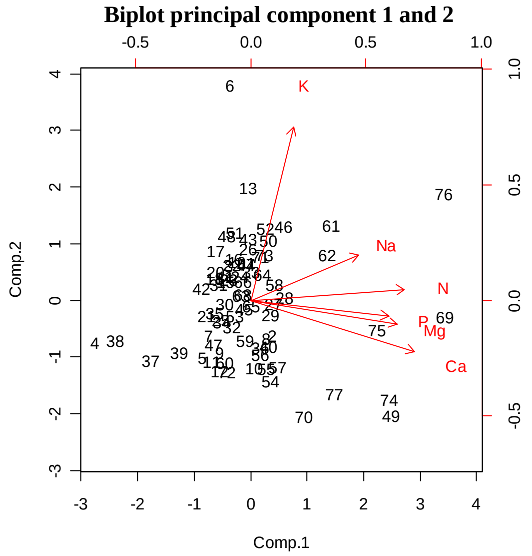


Fig. 2.18: The numbers represent sample number (individuals) of *Alces alces* (moose): 1 to 68; *Cervus elaphus* (red deer): 69 to 73; *Capreous capreolus* (roe deer) 74 to 77. The First principal component expresses 51% of the total variation and the second principal component expresses 17% of the total variation in nutrient and mineral content. The first component is strongly determined by a correlation of N, P, Ca and Mg. The second principal component is determined by the weaker correlation of K and Ca and Mg.

2.2.2 Amount of pellets

The mean number of pellets per pellet heap was 51 (sd = 35). The mean dry mass of a pellet was 2.27g (sd = 1.31g).

2.3 Amount of nutrient input

2.3.1 Pellet deposition

Nutrients deposited by moose in the brushwood and elsewhere, based on plot data are shown in Table 2.9. The nutrient input by moose in brook forest is 1.3 kgN*ha^{-1}*yr^{-1} and 0.2 kgP *ha^{-1}*yr^{-1}, based on transect data.

Table 2.9: Nutrient (N and P) input of moose in brushwood and elsewhere, based on plot data.

Structural vegetation type	Nutrients N (kg*ha^{-1}*yr^{-1})	P (kg*ha^{-1}*yr^{-1})
Brushwood	4.0	0.5
Outside the brushwood	1.7	0.2

2.3.2 Urine deposition

The nutrient input by moose through urination is given in Table 2.10, based on plot data.
The nutrient input by moose in brook forest is 0.14 kgN*ha^{-1}*yr^{-1} and 0.013 kgP *ha^{-1}*yr^{-1}, based on transect data.

Table 2.10: Nutrient input by moose through urination, strongly depending on moose densities.

Site	Moose density Moose*1000ha^{-1}	Amount of Urine l*ha^{-1}*yr^{-1}	N input (kg*ha^{-1}*yr^{-1})	P input (kg*ha^{-1}*yr^{-1})
BNP	3	8.41	0.04	0.004
Outside the brushwood	10	28.03	0.14	0.01
Brushwood	30	84.10	0.43	0.04

Discussion

2.1 Amount of nutrient input

A larger sample size, is needed to ascertain differences in pellet densities between vegetation types, as numbers of fresh pellets, counted on transects and in plots, were very low. *Repetitive* counting and cleaning of pellets in plots would be a good method to be able to assess differences in pellet densities between structural vegetation types, as mentioned by Månsson *et al.* (2011). Nonetheless, no significant difference in fresh pellet density, is found between the structural vegetation types. Hence, it may be concluded that there *is* at least an input of nutrients in brushwood and in alder carr. Moreover, a trend is found, that pellets and rest places seem to cluster, as suggested by Bokdam (2001) and Mouissie *et al.* (2005). Another tendency, suggested in this study, is that rest places and pellets cluster mainly in the brushwood. This trend is supported by Kufeld & Bowden (1996) and Bergström & Guillet (2002), who explain that willow is extensively used for cover by moose. Yet, few rest places seem to occur on edges of alder too, in the same proportion as pellets occurance there. Gebczyńska & Raczyński (1984) mentioned as well that moose in the BNP may hang out on the edges of the alder carr (Fig.2.19). Hundertmark (pers. inf., 2011) suggests that females with calves, more than males, choose habitat with cover to avoid predators. Concerning movements through the area, Timmerman & Racey (1989) state that moose establish regular paths and avoid dense vegetation. By contrast, this study suggests that moose seem to roam through all structural vegetation types, reed being often very dense. While it is remarkably that moose pellets were often clustered with other ungulate pellets, though this was beyond the scope of this study. Though, further investigation on rest places, paths and pellet deposition places is needed, it may be concluded, supported by literature, that mainly the brushwood habitat is used for nutrient deposition.

N concentrations found in pellets of moose were high compared to the N content (5.58gN*kg^{-1} dry matter intake) analysed in pellets from *Cerpvus elaphus nelsoni*, the rocky mountain elk (Hobbs *et al.*, 1982). The *concentration* of N in moose's pellets is twice as high as the adequate concentration analysed in plants and also the P concentration in pellets is high (Raven *et al.*, 2003). Besides, the concentrations of K and Ca in pellets of moose were rather low compared to plant tissue concentrations (Raven *et al.*, 2003). Next to this, roe deer cause a larger input of N an P per dry mass deposited. Besides, a good correlation between the nutrients deposited may indicate that a higher concentration of a certain nutrient in pellets, may imply that the concentration of other nutrients deposited, are higher as well. Considering urine excreted by moose, P concentrations, based on Kaneko *et al.* (2008), were rather low, although, Manston & Vagg (1970) also found low P concentrations in urines from grazing cows.

It has to be mentioned that gaseous nutrient losses from excreta were not assessed in this study. However, ammonia volatilization from deposited urine may range between 10-40% of the total N in urine (Ruess & McNaughton, 1988 in: Uytvanck, 2009). Besides, denitrification from soil organic matter (Fig.1) is another source of gaseous N loss. In addition, Uytvanck (2009) states that gaseous N losses, in the cycle as considered in this study, are in general low.

Conclusion

It may be concluded, supported by literature, that mainly the brushwood habitat is used for nutrient deposition. Besides, few pellets are deposited in brook forests. N and P concentrations in pellets are high, compared to adequate plant concentrations

Fig. 2.19: Moose calf hides on the edges of an alder brook (photo: Sanne Dirickx).

PART 3: NUTRIENT UPTAKE OF EXISTING VEGETATION

Introduction

This part is stated as a hypothesis supported by data, as not enough data were collected to state the results as thoroughly proven facts. The yearly nutrient uptake of existing vegetation is estimated for two reasons. Firstly, the estimation is done, to assess the relevance of the amount of nutrient put in the ecosystem by moose (§ 2.1 and 2.3). Secondly, the amount of nutrients removed from existing vegetation has to be compared with the amount that returns into it. Willow vegetation is the target vegetation to be examined, since brushwood habitats, especially willow shrubs, are mostly used for nutrient deposition and willow, mainly *Salix cinerea*, is the main browse species.

In this study, biomass and nutrient content were only considered "aboveground", despite the the fact that nutrients are also stored in roots (Raven *et al*., 2003). In order to assess the nutrient content of a shrub, primary and secondary growth need to be taken into account. Primary growth is the extension of the plant initiated by the apical system, whereas secondary growth is the thickening of the stem and the roots, resulting from the activity of lateral meristems (Raven *et al.*, 2003).

In general, it is questioned how much nutrients (N and P) are taken up by *Salix cinerea* per hectare per year (which means in the growth season) (§ 3.1.3). Besides, it was tested if N and P content were linked to twig diameter (§ 3.1.2) and to dry mass (§ 3.1.1) as secondary growth is expected to increase with age. If a correlation is found those parameters may be used to predict N and P content.

Method

3.1 Nutrient content of *Salix cinerea*

3.1.1 Nutrient (N and P) content of leaves and twigs per age category

Measurements of *Salix cinerea* shrubs have been collected to determine their N and P content. Data were gathered between the 27th of June and the 1st of July 2011. On four sites, two or four shrubs per site (12 in total) were randomly picked in the neighbourhood of the pellet plots (Fig. I.29) to measure and sample. From a distance, *Salix cinerea*, the grey willow, can easily be recognised by the bluish-grey colour and dome-shape (De Fré & Hoffman, 2004). As browsing implies a loss of nutrients, it was necessary to verify whether or not the shrub was representative: it had at first sight no extreme size, no leaf aberrations and was not (recently) browsed. Then, the number of branches of the shrub was counted (Fig. 3.20). One branch per shrub, representative in length and width, was sampled and cut in twigs according to their estimated age. Since the sampled branch was cut at the base, the maximum age of the shrub could be estimated. Previous apices (Fig.3.20) were used to separate twigs of different age categories (since no precise ages were known). These had been apexes that stimulated growth of multiple branches at the beginning of a new grow season (Raven *et al.*, 2003). As a consequence, every fork upwards was assumed to represent a separation between two growing seasons. Moreover, twigs of less than one year old were recognised as they are felty (densely haired), weak and light brown with soft and rather small leaves (Appendix VII, Fig. VII. 2). Twigs of maximum two years old are tougher, darker coloured and hair on twigs occur less densely. Additionally, all the leaves of a sampled branch were collected. Twigs and leaves of the sampled branches were transported and oven dried at 70°C. Dry mass of twigs was measured per age category, all together at once, to minimize measurement error (ME). Dry mass of leaves per branch was measured as well, since it comprises both primary and secondary growth.

Twigs were grinded to fine dust, per age category and per sampled shrub, and leaves were grinded per sampled shrub too. Chemical analyses of N and P leaves' content and of eight twig age categories (sample sizes: $twig_{<1;\ 1\text{-}2;\ 2\text{-}3;\ 3\text{-}4}$: n = 12; $twig_{4\text{-}5}$: n = 6; $twig_{5\text{-}6}$: n = 4; $twig_{6\text{-}7;\ 7\text{-}8}$: n = 2) were carried out according to Walinga *et al.,* (1989) by a SKALAR*, SAN ^{plus} SYSTEM.

Next, nutrient content and mean dry mass were put in a graph (untransformed) (Fig. 3.21). A Box-Cox power transformation ($\lambda = 0$) was performed for the measured data of the N contents, as the variances were not equal, as shown by a Bartlett test. The data of the P content were normally distributed. Differences between the leaves' and twigs' nutrient content (dependent variable) of different age categories (independent variable) were tested (separately for N and P) with a one-way ANOVA and Tukey (HSD). Differences between N (untransformed) and P content (dependent variable) over the categories (independent variable) were computed by a Kruskal-Wallis test. Spearman Rank correlation tests were completed between N (untransformed) and P content and between N content (untransformed) and dry mass. Parametric correlations were carried out between P content and dry mass. To look at nutrient limitations N/P ratios were computed (Fig. 3.22)

3.1.2 Nutrient content in relation to twig diameter

The diameter of two twigs per age category (of the 12 samples) was measured with an electronic calliper. Per twig the diameter was measured at five places to get a mean per twig. An overall mean per age category was made to take the mean over all (24) measured twigs (Fig. 3.23A). Spearman Rank correlation tests were done between N content and diameter of the twigs. Parametric correlations were conducted between P content and diameter of the twigs. Moreover, to test if N and P content may be estimated measuring twig diameter, prediction intervals were calculated making it able to estimate N and P content for a range of twig diameter values (Fig. 3.23 B and C).

3.2 Estimation of yearly nutrient uptake of *Salix cinerea*

As it has been estimated out how old shrubs approximately are, it is possible to measure how much N, shrubs took up from the beginning of their life until 'sample age'. 'Mean' theoretical shrubs were made, based on mean values of parameters of sampled shrubs in the field (Fig.3.20; Appendix VIII). Only shrubs of 4, 5, 6 and 8 years old were sampled. Consequently, only for these shrubs the mean number of branches per shrub is known. Nevertheless, the estimated number of branches for a shrub of 8 years old was very low and only based on one measurement. Therefore, age category 8 was excluded. Since the mean age category sampled was 4 this was taken as mean shrub age in BNP. The yearly nutrient uptake was calculated for category 4 to 5. As a comparison, yearly nutrient uptake was also estimated for shrubs of age category 5 to 6 to compare (Appendix VIII).

Estimations of numbers of *Salix cinerea* individuals were realised at 13 different sites, after which these countings were extrapolated to a hectare, to estimate the number covering 100% of a hectare (Fig.I.29). As willows typically occur in mosaics (De Fré & Hoffman, 2004), real willow cover per hectare had to be estimated in BNP. On sites indicated in the field as belonging to the structural vegetation type of brushwood (with mainly willows), plots of 100 by 100m (one hectare) were drawn on Google earth and shrub cover was estimated in percentages. The willow cover was estimated for 5 large willow patches and for 5 sites where willows occur in small patches. The mean cover for both subdivisions was calculated and multiplied by the number of willows estimated to cover 100% of a hectare.

To assess the yearly nutrient uptake of willows, a minimum and maximum estimation were made. The minimum estimation assumes that *all* nutrients of the leaves are retreated before the leaves fall. As a consequence, the difference in twigs' nutrients (N and P) of successive years gives the yearly growth (Appendix VI). The maximum estimation assumes that *no* nutrients of the leaves are retreated before the leaves fall (Table 3.11). The difference in twigs' and *leaves***'** nutrients (N and P) of successive years give the yearly growth. As a result, every year nutrients have to be taken up to refill the gap of nutrients lost as leaves are dropped. Yearly nutrient uptake was calculated with the following formula:

Number of shrubs per ha * $\Delta_{\text{nutrient content of successive age categories}}$ (g) (Formule 3.8)

$\Delta_{\text{nutrient content of successive years of shrubs}}$ (g) is the difference in nutrient content between two successive age categories.
Successive steps were taken to calculate nutrient content; starting from nutrient content per twig, then per branch, per shrub and finally per hectare of willow shrubs. All steps taken are explained more in detail in Appendix VIII.
Nutrient stock in living biomass (DM) (Table 3.11) of *Salix cinerea* shrubs was calculated with the formula:

Number of shrubs per ha * $M_{\text{Nu mean } \textit{Salix cinerea}}$ (g) (Formule 3.9)

$M_{\text{Nu mean } \textit{Salix cinerea}}$ (g) is the mean amount of nutrients (N and P) of a 'mean theoretical shrub' of the mean age category.
The production of DM (Table 3.11) was estimated using a 'mean theoretical shrub' of the mean age category's mean percentage of N (g) multiplied by the nutrient stock in living biomass:

(100 / N (%) per shrub) * Nutrient stock in living biomass ($kg*ha^{-1}$) (Formula 3.10) (pers. inf. Van Diggelen, 2011)

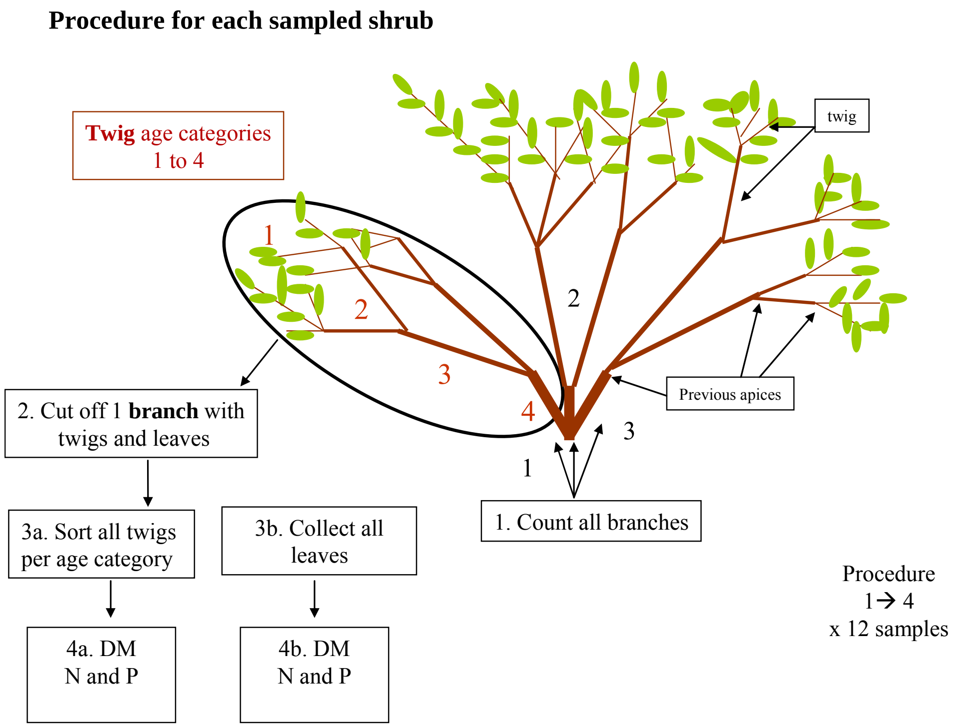


Fig. 3.20: Procedure for each sampled shrub (DM = dry mass).

Results

3.1 3.1 Nutrient content of *Salix cinerea*

3.1.1 Nutrient (N and P) content of leaves and of twigs per age category

Maximum eight age categories were counted per shrub. There is a difference between, on the one hand, age categories in N content ($p < 2.2e\text{-}16$, $F = 51.2$, $df = 8$) and age categories in P content ($p < 2.2e\text{-}16$, $F = 58.6$, $df = 8$) on the other hand. Leaves consist significantly of more N than twigs (Fig. 3.21). But twigs younger than one year old contain significantly more N than the twigs of the older twig categories.

The N content is larger than the P content ($p < 2.2e\text{-}16$, Kruskal-Wallis $\chi^2 = 110.3$, $df = 1$), but both nutrients are very well correlated ($p < 2.2e\text{-}16$, $\rho = 0.83$, $S = 11211$). No significant correlation is found between mean dry mass and N content of the twigs ($p = 0.88$, $\rho = 0.07$, $S = 11$) and P content of the twigs ($p = 0.72$, $\rho = 0.14$, $t = 0.3699$, $df = 7$). The N/P ratios indicate a N limitation as values are beneath 16 (Fig. 3.22) (Koerselman & Verhoeven, 1995).

3.1.2 Nutrient content in relation to twig diameter

No significant correlation is found between twig diameter and N content ($p = 0.24$, $\rho = -0.48$, $S = 124$) (Fig. 3.23 B). A significant strong negative correlation is however found between twig diameter and P content ($p = 0.007$, $\rho = -0.88$, $S = 158$)(Fig. 3.23 C). This means that the P content decreases with age category. Yet, the prediction interval is wide and suggesting twig diameter is not an applicable parameter to estimate N and P content. Moreover, Fig. 3.23 A shows that standard deviations of twig diameters are high, indicating a low reliability.

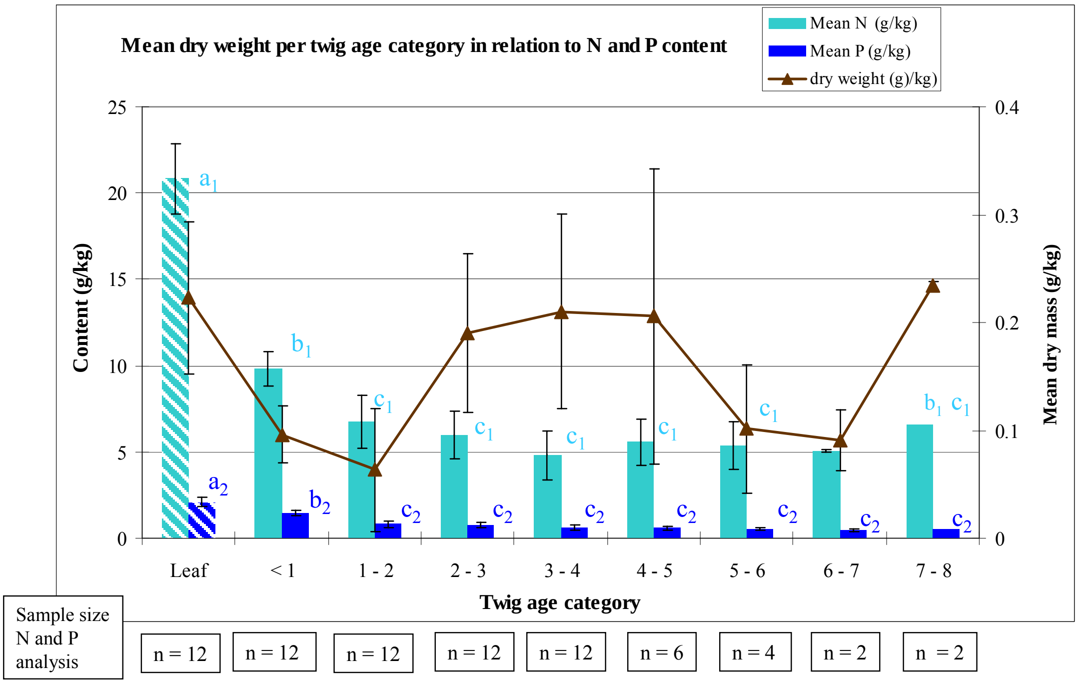


Fig. 3.21: Shows N and P content (g*kg^{-1}) of leaves and twigs per age category. Mean dry mass (g*kg^{-1}) is given for each age category. Different letters (1) show significant differences between N contents of leaves and different twig categories (light blue). Different letters (2) show significant differences between N contents of leaves and different twig categories (dark blue).

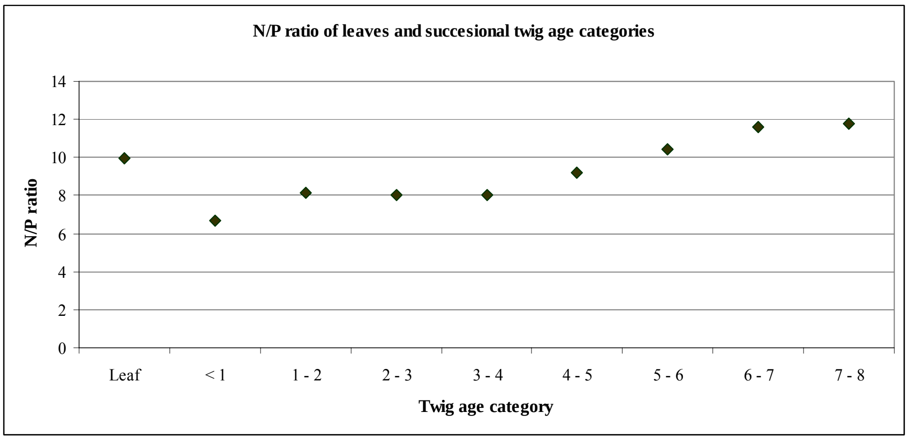


Fig. 3.22: N/P ratio, indicating a N limiation.

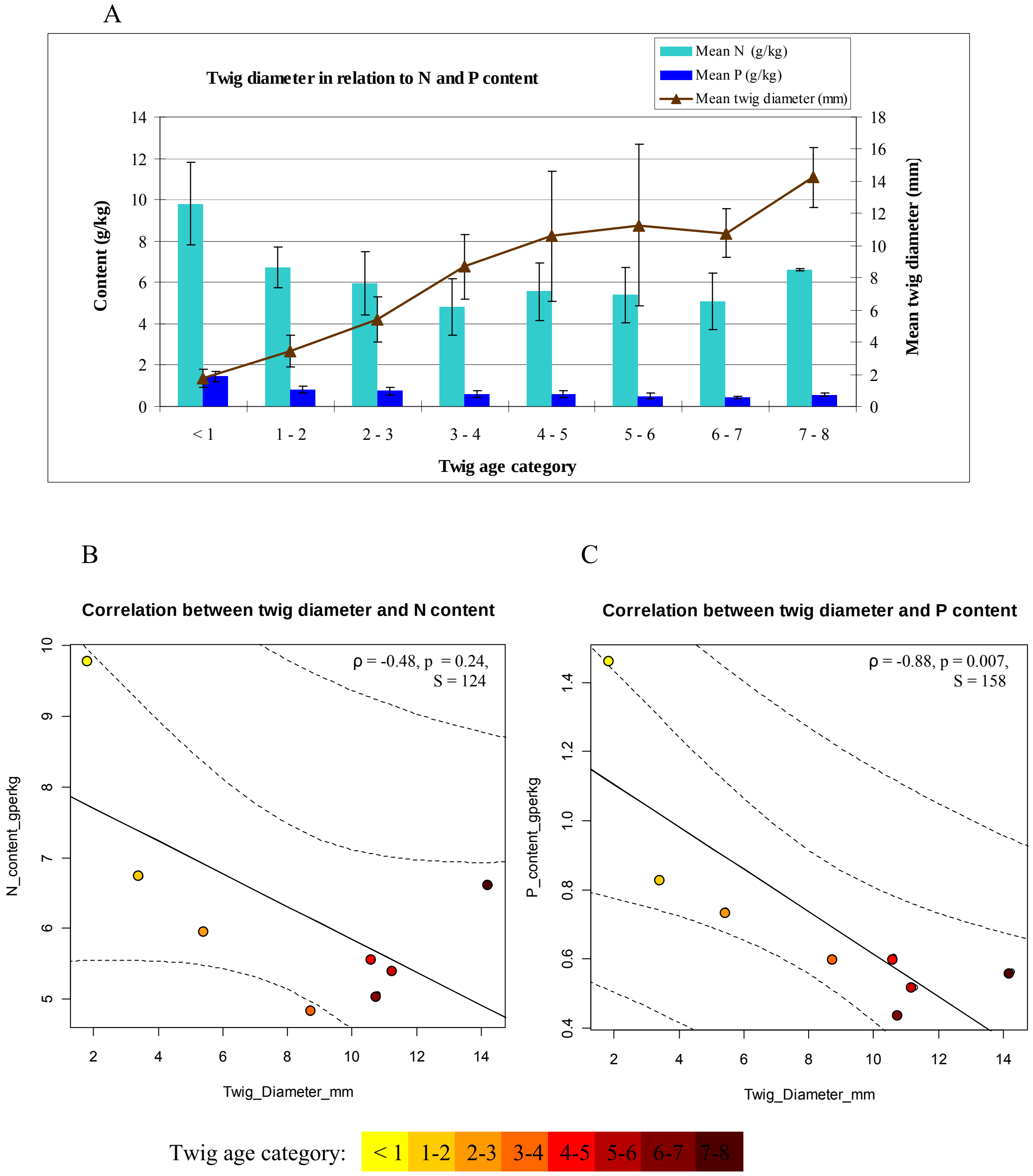


Fig. 3.23: Shows the relation between twig diameter (mm) and nutrient content (N and P). In b and c: full line: regression line; dotted lines closest along the regression line: confidence bands; dotted lines most far from the regression line: prediction intervals.

3.2 Estimation of the yearly nutrient uptake of *Salix cinerea*

A mean of 30223 willows/ha (sd = 33932) was counted for a willow cover of 100%. Whereas large willow patches had a mean cover of 68% resulting in 20552 willows/ha, a mean cover of 33% resulting in 9974 willows/ha was estimated for small willow patches.

Nutrient uptake seems to be not linear, comparing yearly nutrient uptake from 5-4 and 6-5. Mean nutrient uptake (kg*ha^{-1}*yr^{-1}) is given in Table 3.11. Using the N content of a branch and the total mass of a branch, calculations show that a shrub of 4 years old contains a mean of 0.8% N and 0.09% P.

Table 3.11: Minimum (A) and maximum (B) estimations of nutrient uptake ($kg*ha^{-1}*yr^{-1}$) for a shrub from 4 year to 5 year.

Scale of the willow patches	Cover	Nutrient stock in living biomass DM		Production DM	Nutrient uptake			
					Minimum estimation		Maximum estimation	
		N	P		N	P	N	P
	%	$kg*ha^{-1}$	$kg*ha^{-1}$	$kg*ha^{-1}*yr^{-1}$	$kg*ha^{-1}*yr^{-1}$	$kg*ha^{-1}*yr^{-1}$	$kg*ha^{-1}*yr^{-1}$	$kg*ha^{-1}*yr^{-1}$
Large scale	68	189	22	23666	47	5	151	16
Small scale	33	92	10	11485	23	3	73	8

Discussion

3.1 N and P content in willows

The high N and P content in leaves and young twigs may explain the selectivity of in the *parts* of the plants they eat (Bergström and Danell, 1995). Percentages of N and P in *Salix cinerea* seem not to be overestimated as data are similar to a study of Stumph & Wright (2007) (§ 1.3). Leaf N content in this study is high, yet similar to the content of a clone of *Salix* spp., planted to remove nutrients, as explained by Guidi & Labrecque (2010). Furthermore, willow clones are specifically used for their capacity of taking up large amounts of nutrients (e.g. from wastewater) with a view to producing biomass and, as such, to gaining energy (Guidi & Labrecque, 2010).

Twig diameter is rather correlated to N and P content than to dry mass, although none of those parameters seem to be precise enough to predict N and P contents. However, these results need to be treated with caution as sample size was too low to draw profound conclusions.

Willows are N limited, which is not surprising as the system in the BNP is N limited as well (Venterinck *et al.*, 2009). Vascular plants measured by Venterinck *et al.*(2009) were equally N limited .

3.2 Estimation of yearly nutrient uptake of *Salix cinerea*

Willows typically occur in small scale mosaics (De Fré & Hoffman, 2004; Stumph & Wright, 2007), being a commonly present landscape element in the current BNP. Nevertheless, *Salix cinerea* also occur over large areas (De Fré & Hoffman, 2004). In BNP, *Salix cinerea* occupies large patches together with open birch forests and close to the river. The latter may explain the larger nutrient input from the floodplain, giving shrubs the opportunity to spread. Consequently, it seems reasonable to take a large and small scale cover for further investigation.

The nutrient stock in living biomass of willows measured in this study was double as much as the nutrient stock in living biomass of vascular plants measured by Venterinck *et al.*(2009) in some a number of sites of BNP. The latter measured a nutrient stock of 46-65 $kgN*ha^{-1}$ and around 4 $kgP*ha^{-1}$ in undrained fens and around 60 $kgN*ha^{-1}$ and 4-5 $kgP*ha^{-1}$ in floodplains. The difference with the present study may be caused by the fact that willows accumulate nutrients during several years in their living parts. By contrast, herbs and sedges, being part of vascular plants, may only store nutrients from one year in their aboveground parts (Burns *et al.*, 1997).

The productivity estimated in this study is very high, compared to the production measured by Stolarski *et al.* (2011) under optimal growth conditions. Stolarski *et al.* (2011) showed a productivity obtained by agro technology, of 22000 kgDM*ha^{-1}*yr^{-1}, albeit willow clones up to only three years old. Yet they stated as well that the productivity of willows is variable and may range between a few and 30000 kgDM*ha^{-1}*yr^{-1}. In addition, they reported that a realistic yield on production plantations ranges between 4000 and 10000 kgDM*ha^{-1}*yr^{-1}. Yet, a high productivity, unless close to the river, was not expected in BNP considering the low mineralisation rates in the system (Venterinck *et al*., 2009). Nevertheless, it may indicate that productivity differs strongly between vegetation types. However, the productivity may even increase in successive years as shrubs (willow, birch and alder) are expanding in the BNP (Appendix IX,). Indeed, the mean willow density was high and as such, in several places, individual willow shrubs were difficult to distinguish in the field. As a comparison, the mean density was half as much as willow clones planted on rows in energy yield experiments resulting in 20000 plants*ha^{-1} (Mitsui *et al*, 2010) and 24000 plants*ha^{-1} (Stolarski *et al*., 2011). Notwithstanding the *variation* in numbers of willow individuals counted, the numbers were high was very high.

Nutrient uptake does not seem to be linear when comparing differences in shurbs' yearly uptake of successive ages. Since biomass increases every year, more twigs and more leaves are grown every year, resulting more nutrients to be taken up every year. A comparison with nutrients available will be made in the general discussion.

A number of weak points need to be mentioned, indicating that the estimations made in this part need to be treated with caution. In general, more data are needed to draw profound conclusions. In particular, the mean shrub age used is based on few data. Though a mean age is difficult to assess because of the different brush chopping management on different locations, a mean shrub age measured specifically at some sites, along with some other parameters of the site (mineralisation, water level and management), would be most appropriate. In this case, sites may be listed in categories and the production and yearly nutrient uptake may be compared with the shrub ages. In general, yearly nutrient intake may be higher as nutrients in underground parts were not included. This may be especially important as species adapted to floodplain areas may react to water logging by an abundant production of adventitious roots (Guidi & Lambrecque, 2010). Even if the shrubs sampled were not browsed recently, they may have been browsed longer ago, which might have had an influence on the nutrient content of the shrub.

Conclusion

Leaves consist of significant more N and P than twigs and twigs younger than one year old contain significant more N and P than the twigs of older twig categories. Neither twig diameter, nor dry mass per age category is a good parameter to estimate differences in N and P content. Willows in BNP are N limited.

GENERAL DISCUSSION ON NUTRIENT DYNAMICS: SYNTHESIS OF PART 1, 2 AND 3

The *place* of nutrient removal (part 1) and input (part 2) by moose is compared to assess whether or not moose cause a nutrient re-distribution in this fen ecosystem (synthesis 1). A next step consists of assessing whether the *amount* of nutrients put in by moose (part 2) is *relevant* compared to the *amount* of nutrients removed (part 1) and to the *amount* of nutrients released by soil mineralisation and atmospheric deposition. Then, the nutrient *input* (part 2) is compared with the nutrient *uptake* by willows (part 3) (synthesis 2). Also decomposition rates of pellets and litter are compared. Finally, it is discussed whether or not moose enhance or decrease nutrient availability in a fen and thus stimulate or suppress shrub growth (synthesis 3).

Synthesis 1: Do moose cause a redistribution or a recycling of nutrients?

An overview of moose activity in BNP is shown in Fig. 24. Moose forage mainly on shrubs, especially willows. Hence, browsing occurs in brushwood patches, dominated by willows and birches. *Salix cinerea* in particular is highly preferred by moose in BNP, contributing to at least half of its summer diet. Willows create high quality patches in terms of food and horizontal and vertical cover for moose (Kufeld & Bowden, 1996; Bergström & Guillet, 2002). Nutrient input by pellets is mainly concentrated in brushwood as well as rest places. Thus, *Salix cinerea* gets most nutrients back, since removal and input of nutrients by moose are both concentrated in willow vegetation. This implies that a large part of the nutrients are not redistributed, but locally recycled. This is in clear contrast with the hypothesis that pellets are expected to be transported from forage to resting places (Bokdam, 2001; Mouissie *et al.*, 2005). Next to this, a small part of around 1/3rd of the amount of nutrient input by excretion in the brushwood is deposited in the edges of alder carr, suggesting a small part of nutrients is re-allocated.

For cattle it is known that digesting food and dropping the ballast takes up to two days (Cosyns *et al.*, 2005). Counting with this as a constant digestion rate, moose are clearly capable of bringing nutrients from one brushwood “island” to another. However, it is very likely that the amount of nutrient input by moose is proportional to the amount of biomass removed, as the time spent in a patch determines both (Cosyns *et al.*, 2005). The redistribution of nutrients between patches can, therefore, be estimated as extremely small. Nevertheless, more information on the daily patterns of moose movement would clearly enhance our understanding and enable a more accurate and quantitative assessment of nutrient distribution.

Synthesis 2: Nutrient process rates by moose in comparison to willow requirements

Combining the afore-mentioned measured data with literature data on atmospheric deposition and soil mineralisation gives an estimation of the nutrient balance for N and P in *brushwood* (Table 12). Remarkably, the calculated amount of nutrients removed is lower than the input, suggesting a re-allocation of nutrients to the brushwood from (an)other vegetation type(s). In reality, however, I rather found a weak nutrient export to alder woodland.

This suggests that the calculated removal by moose might be slightly underestimated. This may be caused by the assumptions made, especially moose *density*, a main factor with respect to nutrient dynamics (Van der

Graaf *et al.*, 2005), is likely to be underestimated in the dense brushwood. For cattle, N intake is known to be similar to the amount of N excreted (Pfeffer & Hristov, 2005). For ruminants, N is mainly important for fermentation processes, only a very small portion is absorbed (Pfeffer & Hristov, 2005). But as a supplementary amount of N from degraded proteins is excreted, N input and output are equal (Pfeffer & Hristov, 2005). P-intake seems to be even more underestimated in the present study and has as an activating function as well for digestion (Pfeffer & Hristov, 2005).

When removal and input are largely equal in the brushwood, implying an *entire* recycling of nutrients in the brushwood, this suggests that the part of nutrients allocated to alder carr is very small, as suggested in synthesis 1.

Table 12: **Nutrient balance**: summary of the nutrient dynamics with interference of moose in **brushwood** vegetation of a fen ecosystem (BNP) with a moose density of 30 moose*1000ha^{-1}. All numbers are expressed in kg*ha^{-1}*yr^{-1}. Hatched cell: nutrient content unknown. [1]: data of Olde Venterink *et al*., 2009; [2] data of Wassen *et al*., 2005. Percentages of the willow patches, indicate cover per hectare.

Nutrient dynamics	Source	Specification	**N (**kg*ha^{-1}*yr^{-1}**)**			**P (**kg*ha^{-1}*yr^{-1}**)**		
removal	by moose		3.2			0.32		
input	by moose	pellet	4			0.7		
		urination	0.43			0.04		
	by atmosphere		5 - 10 [2]			▨		
		site	undrained	drained	floodplain	undrained	drained	floodplain
	by soil mineralisation		0 – 4 [1]	27 [1]	35 [1]	7 [1]	65 [1]	8 [1]
total input			9 - 18	36 - 41	44 - 49	8	66	9
uptake	by willows	small patches (30%)	23 - 73	23 - 73		3 - 8	3 - 8	
		large patches (70%)		47 - 151	47 - 151		5 - 16	5 - 16

The main question to be answered is whether or not the *amount* of nutrients processed by moose is *relevant* compared to the quantities released by soil mineralisation and from atmospheric deposition. Eutrophication by atmospheric deposition is low in BNP compared to Western Europe (Wassen *et al*., 2005), amounts deposited range between 5-10 kgN*ha^{-1}*yr^{-1} (Table 12). Mineralisation rates of unmown sites, as measured by Olde Venterink *et al.* (2009), show that P input by moose is not relevant in comparison to the amount of P released yearly by soil mineralisation. The input of N, however, is relevant, especially in the undrained brushwood sites where the amount of N processed by moose exceeds the amount released by soil mineralisation and is not much lower than the annual atmospheric N-deposition. Large parts of the catchment area in BNP consist of undrained areas (Olde Venterink *et al*., 2009), suggesting moose have a large impact on nutrient availability in these sites. In floodplains, on the contrary, the effect of moose on N-dynamics is less important because the other N sources are much larger (Olde Venterink *et al*., 2009). Moose prefer to browse and rest in drier places in the area, so-called “silted islands”, small high spots in the fen. The mineralisation rate of such spots is likely to be similar to drained sites and is probably much higher than nutrient input by moose. This would mean that moose have a rather low impact on these spots.

The yearly nutrient supply from the different sources (Table 1) is available for uptake by willows. The total input of P is high enough in the considered sites in BNP measured to fulfill the yearly P requirements of willows. The N-supply per year is also high enough in all three sites for a willow cover of 30% (Table 1). Yet, the calculated yearly N requirement for a willow cover of 70% is even hardly available in the productive floodplains. The minimum value, assuming that all N from the leaves is retreated before they are dropped, seems to be just available. The discrepancy between willow requirement and availability may partly be explained by taking into consideration that the sites with 70% shrub cover are actually more visited by moose than sites with a 30% cover. More time is spent to consume biomass and thus more nutrients are dropped as well. If the input by moose is assessed to be twice as high, the minimum willow requirements would be attained in floodplains. However, this still means that *Salix cinerea* has to be very efficient in mobilising existing reserves to sustain production (Burns *et al.*, 1997) and in taking up nutrients. Uptake efficiency may be enhanced by a symbiosis between *Salix cinerea* and mycorrhizal fungi (De Fré & Hoffman, 2004; Sumorok & Kiedrzynska, 2007). The associated fungi increase the plants' ability to capture water and essential elements, especially P (Raven *et al.*, 2003). The inflow of P measured by Sanders *et al.* (1983 in: Kung'u , 2004) in a P limited montane ecosystem was 2-5 times higher in mycorrhiza roots than in non-mycorrhiza roots. Moreover, such symbiosis might lead to enhanced N uptake as well (Raven *et al.*, 2003). However, only few of such associations occur in wet soils (De Fré & Hoffman, 2004) and Good *et al.* (1992) even stated that willows in waterlogged soils had no mycorrhizae, whereas those in a dryer environment did. Summarizing, *Salix cinerea* may profit optimally from easily available nutrients in litter and pellets and enhances nutrient *availability* locally through mycorrhizal symbiosis. Further research is, however, necessary to confirm that these associations occur in BNP. Also nutrient retrieval efficiency from senescing leaves needs further investigation.

Although moose deposit nutrients in a habitat, nutrient input by moose is only relevant when they are available for plants. On a mud-flat it was observed that less than 1/3rd of cow heaps remain after 200 days (pers. inf. Bakker J. P., 2010) but there are large differences in such values. B. D'hondt (pers. inf., 2010). found a range from 35 to 520 days for cow heaps to be decomposed completely. Because cows are *grazers,* their food may be more easily digested than browse forage (Cederlund & Nyström, 1981). Yet, it seems reasonable to assume that nutrients from moose pellets are available for plants within a year. However, the decomposition rate of pellets is very variable and depending on soil, insects, fungi, food, composition of pellets (pers. inf. D'hondt B., 2010) and climate (pers. inf. Bakker J. P., 2010). Much rain may cause pellets to be decomposed after a couple of weeks, whereas dry conditions may cause pellets to remain much longer (pers. inf. Bakker J. P., 2010). No studies were found on the quality of litter of *Salix cinerea* and the indirect effect of selective browsing on litter quality is unknown. The impact of trampling was clearly visible in the field, suggesting that moose enhance litter decomposition by trampling. Bokdam (2001) even found that the effect of trampling on litter decomposition is most substantial in woody vegetation. Moreover, a combination of pellets and soil trampling seems to stimulate N mineralisation (Pastor *et al.*,1993).

Synthesis 3: Do moose suppress or stimulate shrub growth?

Because nutrient removal and input are almost equal in brushwood, it can be concluded that the nutrient input by moose excretion, compensates for foraging losses. In addition, a faster recycling of nutrients may even lead to a stimulation of brushwood expansion, albeit the shrubs are not able to grow much higher. Individual shrub productivity may not increase much, but more individuals may contribute to the total productivity.

Nutrient changes on a local scale may affect succession on a large scale (Bokdam, 2001). At a small scale nutrients become available soon rather than being stored in only *some* individuals. In this way expansion may be stimulated by redistribution *within* a brushwood patch. Some shrubs lose nutrients whereas others – among which seedlings – can catch up (Bokdam, 2001) (Fig. 24). Spreading and germination may be facilitated by trampling, causing gap formation (Bokdam, 2001). In such ecosystems, nutrients may not be easy to get otherwise (Bokdam, 2001). Moreover, willows grow fast (Bergström & Guillet, 2002) in humid mesotrophic and eutrophic conditions (De Fré & Hoffman, 2004). Sedges and herbs, adapted to nutrient limited conditions, will be outcompeted *locally* (Bokdam, 2001). Uneven browsing and nutrient redistribution within brushwood patches inevitably leads to small-scale mosaics with *local* invasions (Bokdam, 2001). In this way, differing resource levels in gaps, due to herbivory, cause plant succession (Bokdam, 2001). Schmidt *et al.* (2000) describe how such local invasions may contribute to an overall succession. Surface expansion of willow and birches occur when, during a short period of time, a large amount of easily available nutrients is mobilised. Stimulation of birches is probably even larger than that of willows, because birches are consumed less by moose. Nutrients deposited on the edges of alder carr, though, may stimulate the growth of willows there, typically occurring on edges of alder carr (De Fré & Hoffman, 2004) (Fig. 25). Willow shrubs, close to alder carr, are outcompeted over time by alder brook due to overshadowing (De Fré & Hoffman, 2004). Brushwood localised in open fen is the climax vegetation when the soil is not stable enough to hold the larger and heavier alder trees (De Fré & Hoffman, 2004). In short, moose foraging on willows might thus cause a further forestation (De Fré & Hoffman, 2004) (Fig. 26). However, more studies are required to look at multiple effects of stimulation and suppression over time and the effect of changing moose densities. Similar results of stimulation were found by Bokdam (2001) and Van der Wal & Brooker (2004) in an arctic ecosystem, where grasses were stimulated by excretion, despite losses caused by herbivory of reindeer and goose.

In contrast to findings of Olff & Ritchie (1998), who argue that large herbivores are able to increase plant diversity by creating heterogeneity, the present study suggests that moose rather decrease plant diversity by stimulating brushwood expansion. The herbaceous layer in *Salix cinerea* bushes is mostly relative species poor, mainly consisting of marsh plants (De Fré & Hoffman, 2004). As an exception, some threatened macrofungi live on the wood of *Salix cinerea* (De Fré & Hoffman, 2004). A study of Pellerin *et al*. (2006) also stated that high densities of white-tailed deer may have a negative influence on the plant diversity of peat lands in the long term.

In the light of the shrub encroachment that BNP struggles with, moose may not be a good restoration tool to suppress reforestation proposed by Schmidt *et al*. (2000) and Middleton *et al*. (2006). This implies that active and intensive management is required to keep the area open, next to measures to decrease drainage. Prins (1998) states that since the extinction of mega herbivores, such as the forest elephant and the mammoth, towards the end of the Pleistocene (Roberts, 2008), it is no longer possible to keep the vegetation open in Europe. He explains that the remaining large herbivores, like moose and red deer, are not such "bulldozer herbivores".

GENERAL CONCLUSION

Nutrients are not redistributed by moose, but they are mainly locally recycled in the brushwood. Especially in undrained sites, moose have a substantial impact on N dynamics. Despite causing mechanical damage, enhanced nutrient recycling by moose may stimulate brushwood expansion, thus enhancing brushwood cover.

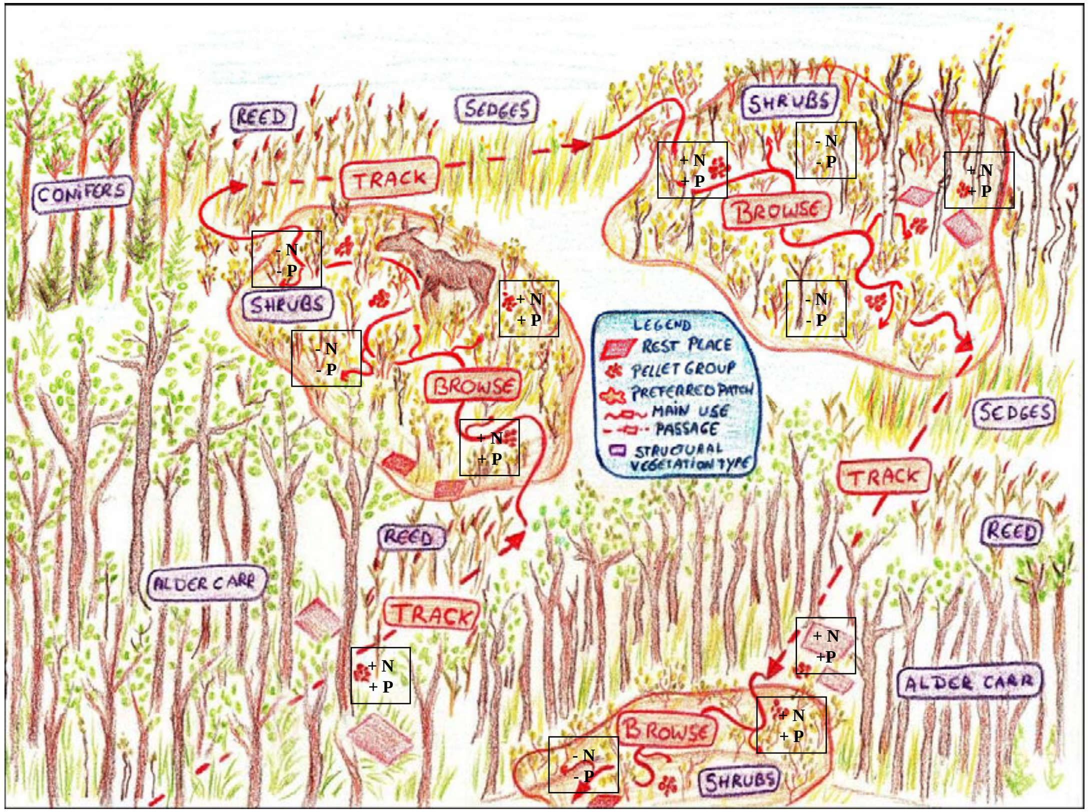


Fig. 24: Summary of moose activities in structural vegetation types.

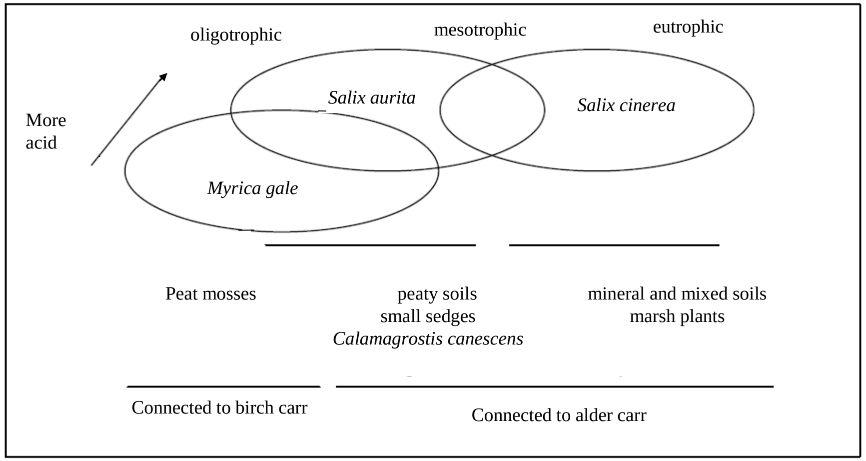


Fig. 25: Summary of mutual associations of groundwater dependent shrubs with respect to nutrient supply, acidity and soil characteristics (Figure adapted from De Fré & Hoffman, 2004).

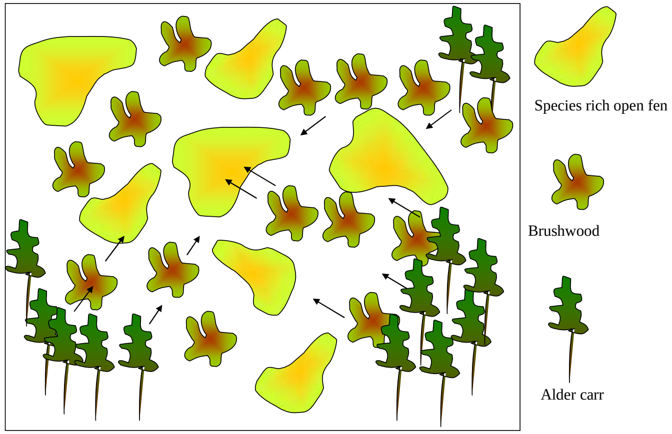


Fig. 26: Spontaneous succession of vegetation in a fen ecosystem.

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http://www.biebrza.org.pl/index.php?strona=152, [11/12/2011]

Photo on the front page:

http://www.google.be/imgres?q=Biebrza+park+narodowi&um=1&hl=nl&sa=N&qscrl=1&nord=1&rlz=1T4SKPB_nlBE296BE297&biw=1280&bih=544&tbm=isch&tbnid=9IYTP28HHvuXRM:&imgrefurl=http://www.splywy.pl/biebrza/&docid=nVJrTUo5MZOMtM&imgurl=http://www.splywy.pl/jpg/biebrza1.jpg&w=288&h=230&ei=mrTxTsqoFoSg-wbe8fCaAQ&zoom=1&iact=rc&dur=342&sig=102927239536124229738&page=1&tbnh=145&tbnw=182&start=0&ndsp=10&ved=1t:429,r:3,s:0&tx=99&ty=108

Map Poland appendix I
http://www.google.be/imgres?q=biebrza+national+park&um=1&hl=nl&sa=N&rlz=1T4SKPB_nlBE296BE297&biw=1280&bih=544&tbm=isch&tbnid=L4ZYZVYcoumCFM:&imgrefurl=http://www.skyscrapercity.com/showthread.php%3Ft%3D859180%26page%3D11&docid=I_p4VDmQwbiihM&imgurl=http://www.dubielvitrum.pl/img/mapki/mapa_polska_podlaskie.gif&w=480&h=445&ei=h7fxToGQG5CE-wa88eTDAQ&zoom=1&iact=rc&dur=457&sig=102927239536124229738&page=2&tbnh=142&tbnw=153&start=10&ndsp=11&ved=1t:429,r:9,s:10&tx=82&ty=72

APPENDIX I: MAPS OF THE STUDY SITE

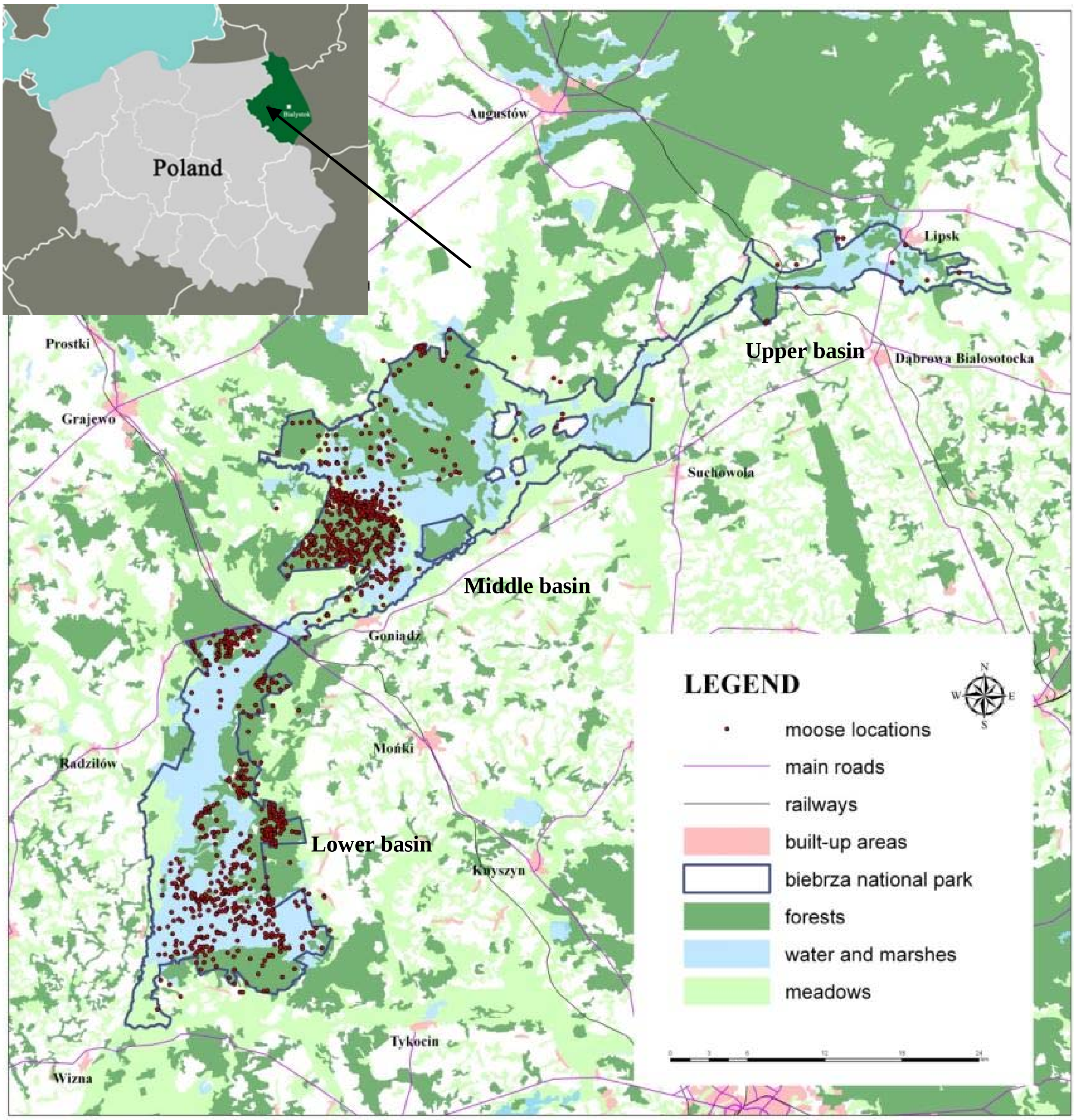
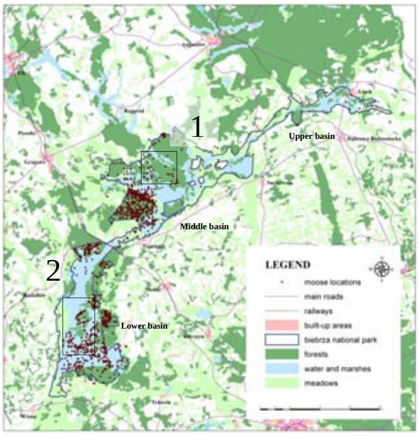
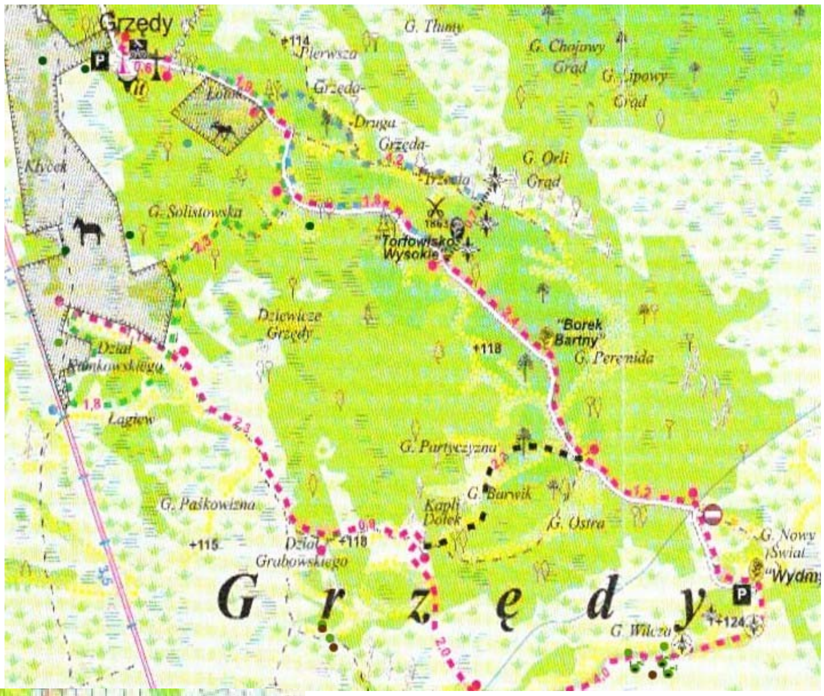


Fig. Map I. 27: Map of moose distribution in the Biebrza National park, based on observations (map: pers inf. of Borowik T., 2010). A higher density of moose location points does not *per se* mean that moose were more abundant there. As different observers were taking part in the monitoring, bias occurred caused by differences in observer engagement. For example, observational bias occurred resulting in a higher density of moose in areas where it was easy to get into the field. (pers. inf. Borowik T., 2010)

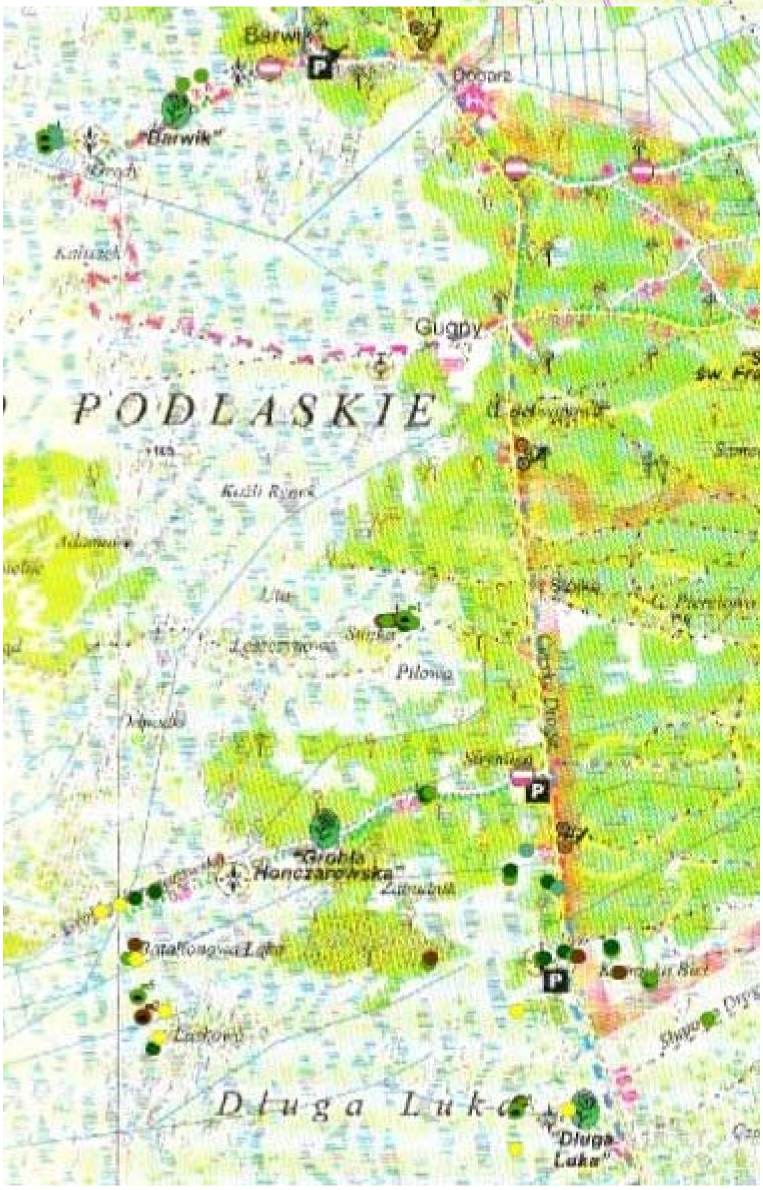
Situation of transects



1



2

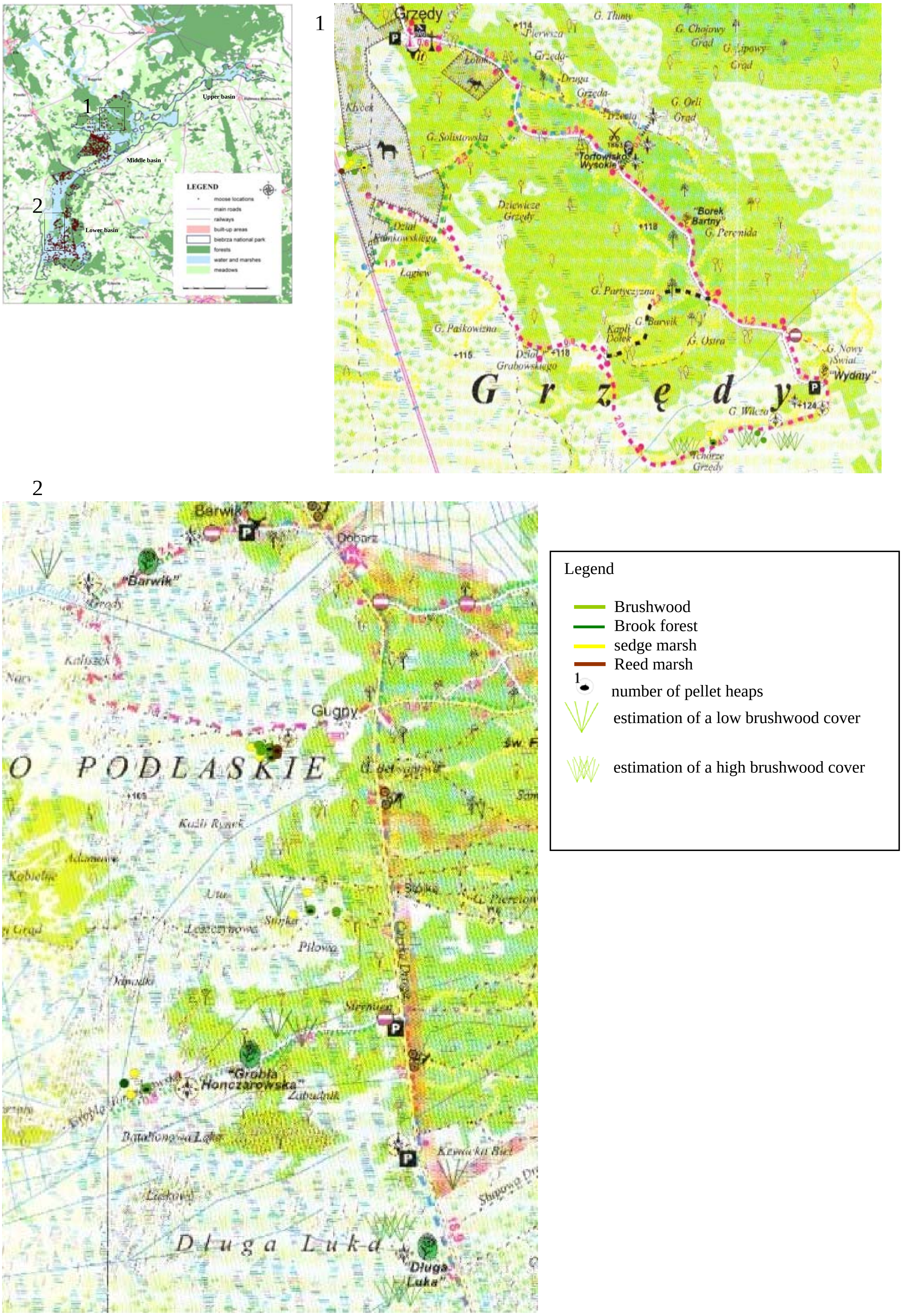


Legend

- ● Brushwood
- ● Coniferous forest
- ● Brook forest
- ● Sedge marsh
- ● Reed marsh
- 1 number of pellet heaps
- □1 number of rest places

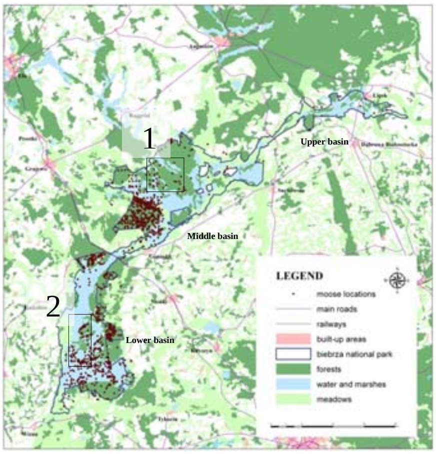
Map I.28: Data on moose, collected on transects to investigate: diet, diet selectivity, pellet density, rest places and paths.

Situation of plots

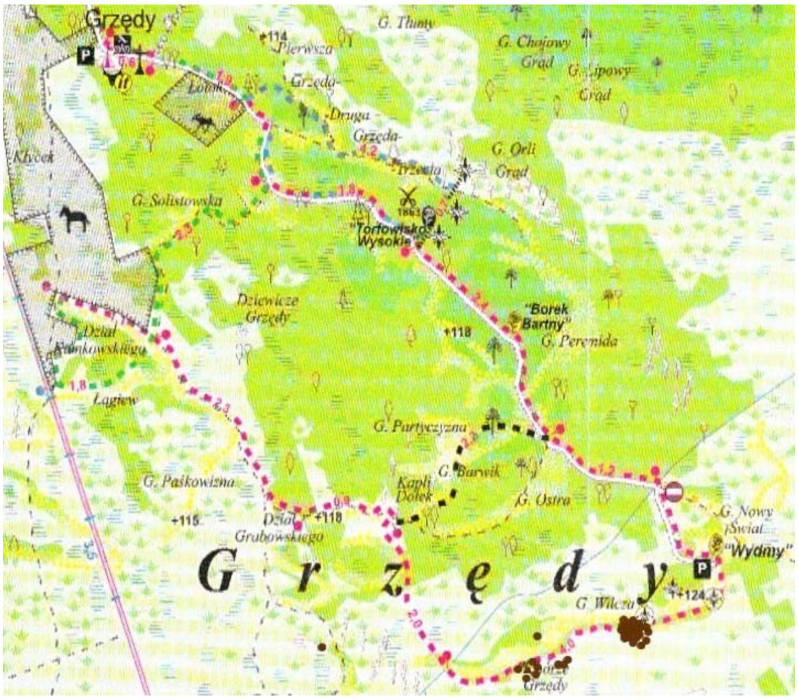


Map I.29: Data on moose, collected in plots to investigate pellet density.

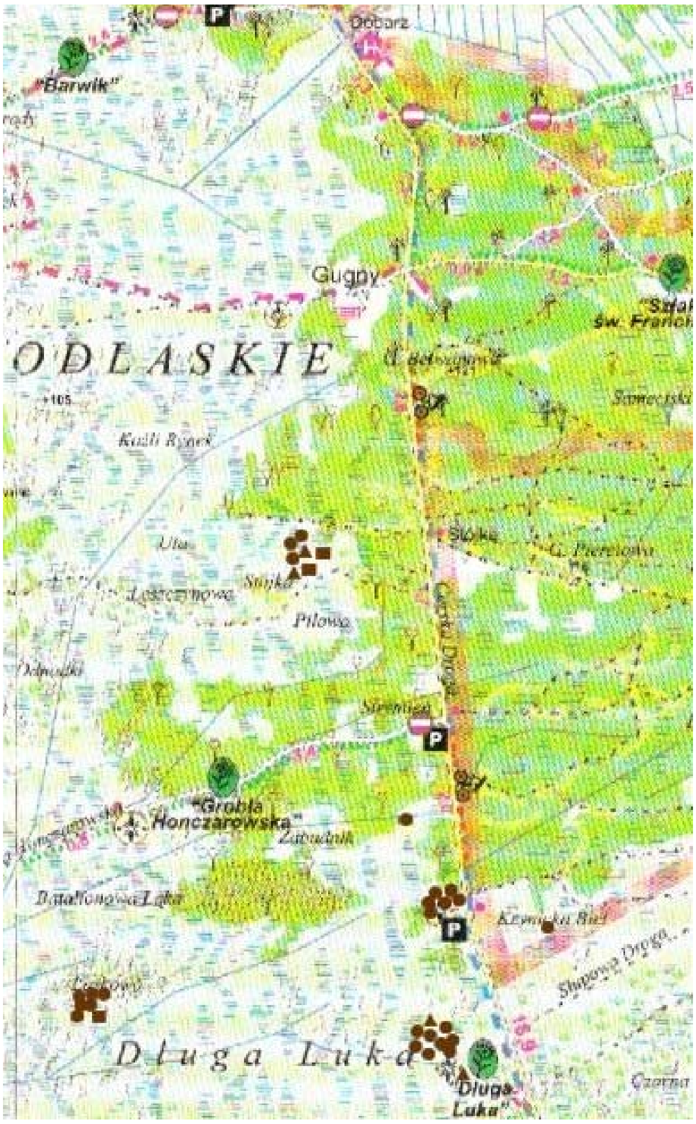
Situation of pellet samples



1



2

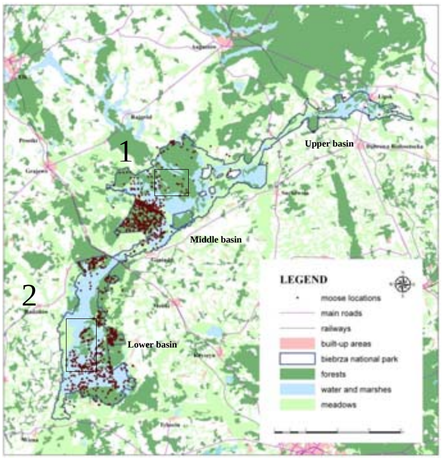


Legend: pellets from

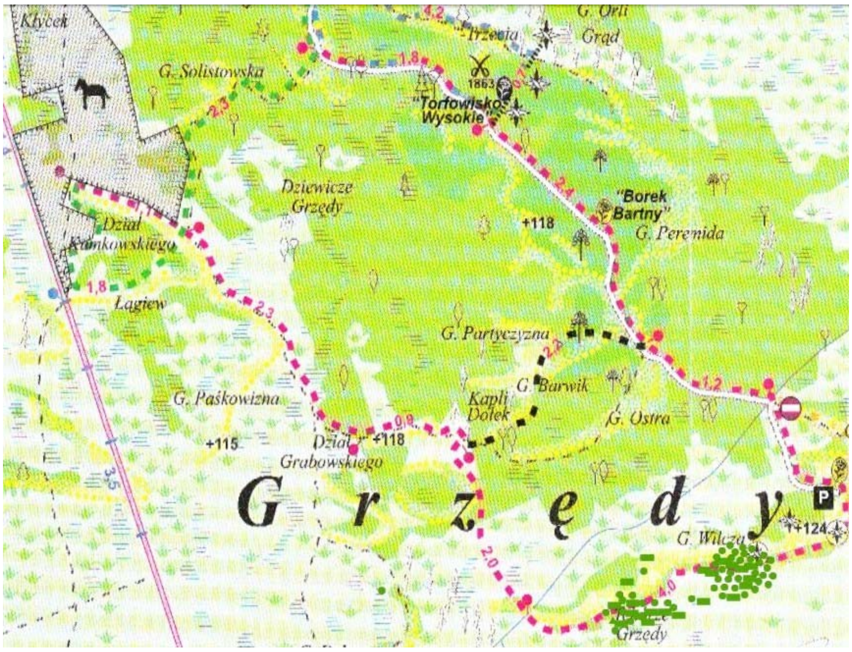
● moose (*Alces alces*)
▲ red deer (*Cervus elaphus*)
■ roe deer (*Capreolus capreolus*)

Map I.30: Data on moose, collected on sites: pellet samples for microscopic diet analysis and nutrient concentrations, 4 samples, collected in the upper basin, were not shown.

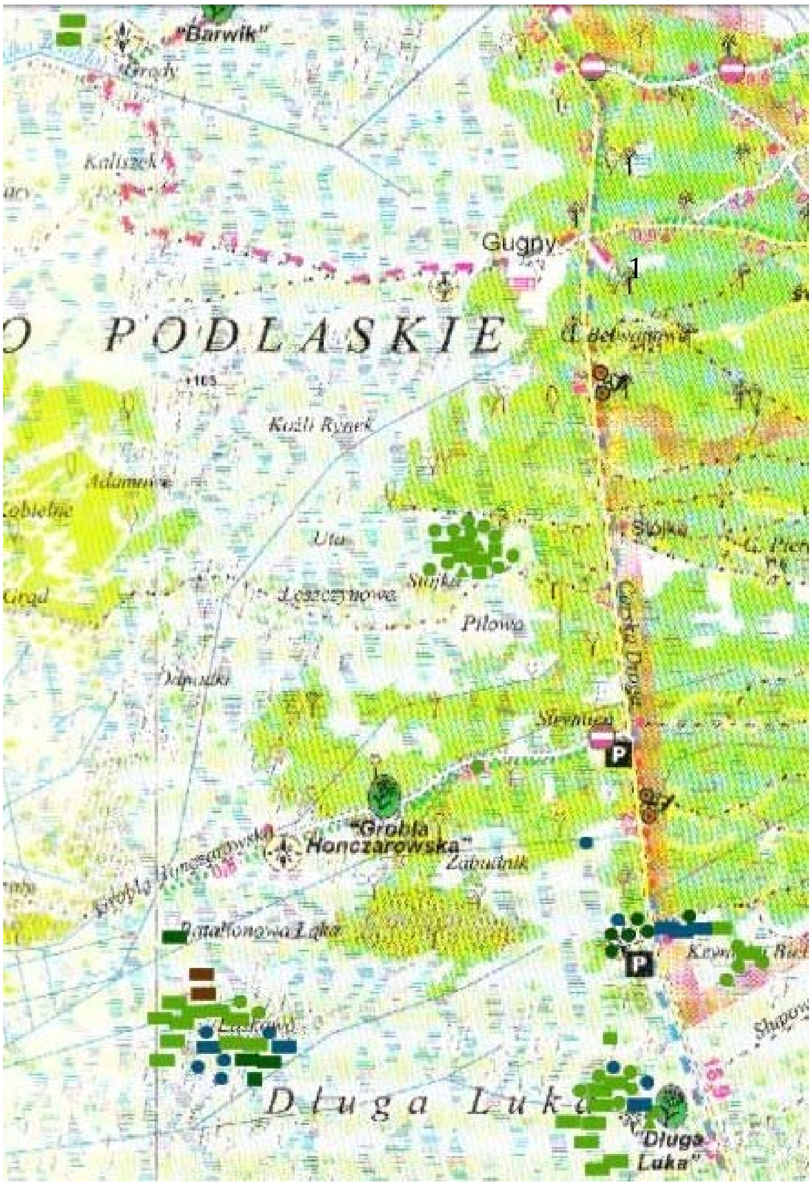
Situation of pellets and rest places gathered on transects, plots and besides



1



2



Legend

━ Brushwood
━ Edge between brushwood and alder carr
━ Brook forest
━ unspecified
○ moose pellet
△ red deer (*Cervus elaphus*)
⌐ roe deer (*Capreolus capreolus*)
▭ rest place

Map I.31: Data on moose, collected transects, plots and besides, when coming across. This map suggests that pellets and rest places are clustered

APPENDIX II: ILLUSTRATIONS ON THE METHODS OF PART 1 AND 2

Fig. II.32a: Left: a fresh (summer) moose pellet heap; right on top: an old (winter) pellets of moose (largest brownish) and red deer (smaller blackish). Right under: roe deer pellets are rounder, smaller and more sticky than red deer pellets.

Fig. II.32b: Left: detail of *Salix cinerea*, demonstrating the leaves' appearance. Right: brushwood, dominated by willows and signs of trampling by moose, showing the appearance of young willow shrubs.

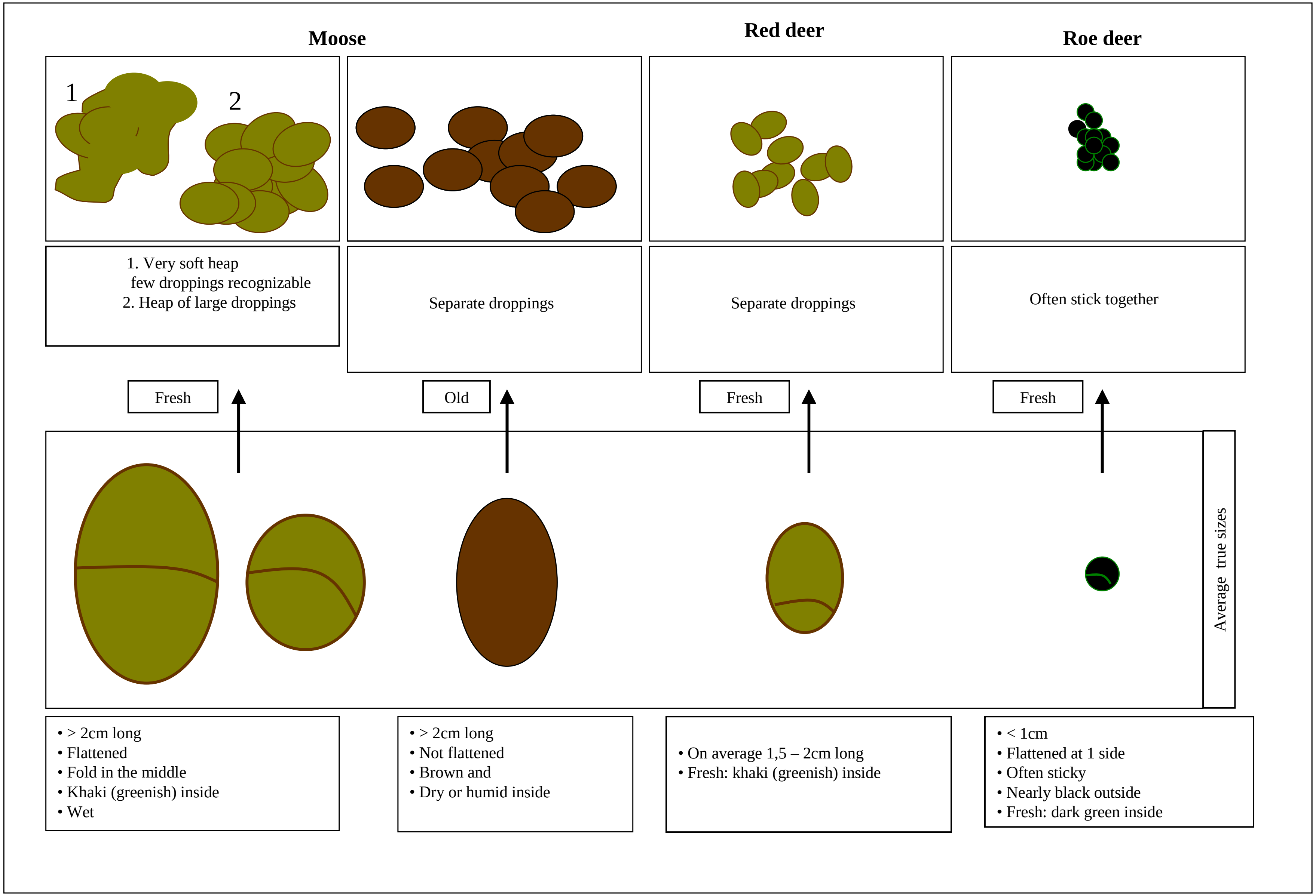


Fig II.32: Key to distinguish moose, red and roe deer pellets and pellet groups. For moose, both fresh and old pellets and pellet groups are given, for red and roe deer only the fresh ones are showed, but the old ones have the same characteristics as listed for each species, but in brownish (red deer) and blackish (roe deer) variants (Brown *et al.*, 2009).

II.34: Epidermises of plant species are needed to study the epidermis cells, making it able to identify cells found in pellet samples. To be able to tear of the epidermises, often a procedure was needed.

Structural vegetation types:

Brushwood

- dominated by willow (mainly *Salix cinerea*) and birch species, with sedges in between the shrubs
- shrubs are concentrated together, on average they are >1m
- open birch forests with shrubs as understory belong to this type, because a lot of willow and birch shrubs occur.

Sedge marsh

- sedges are dominating, herbs occur; if shrubs occur, they are scattered and they are < 1m)

Reed marsh

- reed is dominating, only few shrubs occur
- birch forests with reed (mostly tall) as understory belong to this type

Brookforest*

- Alder or birch brook, with sedges, water plants and *Frangula alnus* as understory

Coniferous forest

- Conifers: old and young stands

* When dense patches of *Salix cinerea* brushwood occured within an alder carr, it was considered as brushwood.

Fig. II.35 Representing of structural vegetation types.

APPENDIX III: TABLES ON THE CALCULATION OF NUTRIENT REMOVAL BY MOOSE

Table III.13: Nutrient removal (kg*ha^{-1}*yr^{-1}) by moose, calculated for a moose density of 3 moose*1000ha^{-1}. Hatched cells indicate different units.

Species or plant category	proportion of diet	Biomass removal (kg*ha^{-1}*yr^{-1})	N content	P content	Units of N and P content	N removal (kg/ha/yr)	P removal (kg/ha/yr)
Salix spp.	0.62	4.0	51.4 *	3.6 *	g*kg^{-1} DM	0.206	0.014
Betula spp.	0.05	0.3	0.016 [1]	0.002 [1]	proportion of DM	0.005	0.001
Populus tremula	0.02	0.1	12.5 [2]	1.25 [2]	g*kg^{-1}DM	0.001	0.0001
Sorbus aucuparia	0.01	0.1	1 [3]	0.1 [3]	proportion of DM	0.074	0.007
Twigs	0.08	0.5	31.95 [4]	2.425 [4]	g*kg^{-1}DM	0.016	0.001
Sedges, grasses and reed	0.17	1.1	10.2 [5]	1.2 [5]	g*kg^{-1} DM	0.011	0.001
Herbs	0.05	0.3	13.9 [6]	2.0 [6]	g*kg^{-1} DM	0.005	0.001
Total	1.00	6.4				0.318	0.026

Table III.14:Nutrient removal (kg*ha^{-1}*yr^{-1}) by moose, calculated for a moose density of 10 moose*1000ha^{-1}. Hatched cells indicate different units.

Species or plant category	proportion of diet	Biomass removal (kg*ha^{-1}*yr^{-1})	N content	P content	Units of N and P content	N removal (kg/ha/yr)	P removal (kg/ha/yr)
Salix spp.	0.62	13.4	51.4 *	5.7 *	g*kg^{-1}DM	0.687	0.076
Betula spp.	0.05	1.0	0.016 [1]	0.002 [1]	proportion of DM	0.017	0.002
Populus tremula	0.02	0.3	12.5 [2]	1.25 [2]	g*kg^{-1}DM	0.004	0.000
Sorbus aucuparia	0.01	0.2	1 [3]	0.1 [3]	proportion of DM	0.248	0.025
Twigs	0.08	1.7	31.95 [4]	3.475 [4]	g*kg^{-1}DM	0.055	0.006
Carex spp.	0.17	3.6	10.2 [5]	1.2 [5]	g*kg^{-1} DM	0.037	0.004
Herbs	0.05	1.1	13.9 [6]	2.0 [6]	g*kg^{-1}DM	0.016	0.002
Total	1.00	21.40				1.062	0.116

Table III.15: Nutrient removal in the brushwood (kg*ha^{-1}*yr^{-1}) by moose, calculated for a moose density of 30 moose*1000ha^{-1}.

Species or plant category	proportion of diet	Biomass removal (kg*ha^{-1}*yr^{-1})	N content	P content	Units of N and P content	N removal (kg/ha/yr)	P removal (kg*ha^{-1}*yr^{-1})
Salix spp.	0.62	40.1	51.4 *	5.7 *	g*kg^{-1} DM	2.062	0.229
Betula spp.	0.05	3.1	0.016 [1]	0.002 [1]	proportion of DM	0.050	0.006
Populus tremula	0.02	1.0	12.5 [2]	1.25 [2]	g*kg^{-1} DM	0.012	0.001
Sorbus aucuparia	0.01	0.7	1 [3]	0.1 [3]	proportion of DM	0.743	0.074
Twigs	0.08	5.1	31.95 [4]	3.475 [4]	g*kg^{-1}DM	0.164	0.006
Carex spp.	0.17	10.8	10.2 [5]	1.2 [5]	g*kg^{-1} DM	0.110	0.004
Herbs	0.05	3.4	13.9 [6]	2.0 [6]	g*kg^{-1} DM	0.047	0.002
Total	1.00	64.20				3.187	0.323

Notes

Data on species and percentages of diet

Percentages contributing to the diet (§ Table 1.3), ^{m} = % of microscopic data, ^{t} = % from transect data;

Tree species

Betula spp.: *Betula pubescens* ^{m}, *Betula pendula*^{t}, pendula humilis^{t}
Salix spp., *S. nigrican* ^{t}, S. *pentandra* ^{m}, *S.repens* ^{m}, *S. triandra*^{t}, *S. caprea*^{t}
Populus tremula^{t}
Sorbus aucuparia ^{m}

Sedges, grasses and reed ^{m}

Carex spp.: *C. appropinquata*, *C. elata*, *C. lasiocarpa, C. nigra, C. rostrata, C. acuta* and one reed species was included in the mean *Phragmites australis,* no grasses were included (Appendix Table …)

Herbs ^{m}

Herbs*: Caltha palustris, Menyanthes trifoliate, Potentilla palustris , Equisetum fluviatile, Thelypteris palustris*

Nutrient data (details: Table IV.3)

Tree species

[1]*Betula* spp.: data (% of DM) from Cederlund & Nyström (1981)

* *Salix* spp.: data of *Salix cinerea* from this study was used for all *Salix* species (§ results 3.1.1)

[2]*Populus tremula*: Mean N content (g/kg) of *leaves* of data from Hobbs *et al.* (1982) and Spalinger et al. (2010), P content was calculated by dividing the N content by 10 (mean N:P ratio from *S. cinerea* and *Carex* spp.)

[3]*Sorbus aucuparia* Mean N content (% of DM) of data from Shipley et al. (1998) and Lundberg et al. (1990), P content was calculated by dividing the N content by 10 (mean N:P ratio from *S. cinerea* and *Carex* spp.)

[4]Twigs: N and P content were calculated by taking the mean of the contents of *Salix cinerea* and *Populus tremula*

[5]Sedges, grasses and reed (data from Biebrza NP, 2010: pers. inf. M. Bormans, 2011)

[6]Herbs (data from Biebrza NP, 2010: pers. inf. M. Bormans, 2011)

Daily food intake

Table III.16: Food intake of moose

Biomass intake	Units	season	Reference
10	kg DM of an adult moose	summer	Renecker & Hudson, 1985 in: Persson *et al.*, 2000
6.5	kg DM of an adult moose	summer	Miquelle, 1983 in: Persson *et al.*, 2001
7.1	kg DM of an adult moose	summer and winter	Persson *et al.*, 2000
$2.5 - 3.2 * 10^9$	kg DM*yr/350000 moose	summer and winter	Persson *et al.*, 2000
20 - 40	kg DM*ha^{-1}*yr^{-1} (*180 moose*ha)	summer and winter	Pastor *et al.*, 1998 (*De Jager & Pastor, 2009)

Moose density

Table III.17: Number of moose over the years in the Biebrza National Park (area = 170 000 ha (park) [5]; 270 000 ha (park + adjacent areas)[6].
Data from: [1]Gebczyńska & Raczyński, 1992; [2]Gebczyńska & Raczyński, 1983 in: Borkowska & Konopko, 1994; [3]Raczyński, 1994; [4]Gebczyńska & Raczyński, 1984; [5]Gebczyńska & Raczyński, 1993 in: Borkowska & Konopko, 1994; [6]pers. inf. Wiktor Kotowski, 2009

Period	Estimated number of moose	Harvest	Mean moose density (individual*1000ha^{-1})	vegetation type	season
1976	670 [1]	120 [1]	-	-	-
1977	720 [1]	170 [1]	-	-	-
1978	821 [1]	170 [1]	-	-	-
1979	800 [1]	170 [1]	-	-	-
1980	810 [1]	200 [1]	-	-	-
1981	770 [1]	200 [1]	-	-	-
1982	780 [1]	300 [1]	-	-	-
1983	620 [1]	290 [1]	3.1 - 5.0 [2] 2.27 [3]	pine and alder forest [2] all [3]	winter [2] mean over the year [3]
1984	570 [1] /800 [4]	200 [1]	10 [4]	marshes and pine forest [4]	summer and winter [4]
1985	480 [1]	210 [1]	-	-	-
1986	620 [1]	250 [1]	-	-	-
1989 - 1991	500 to 600 [5]	-	-	-	-
2009	600 [6]	-	10 [6]	-	-

Nutrient intake by moose

B. Other deciduous tree species

Table III.18: Data from other studies on nutrient (N and P) content and digestibility of tree species, contributing to the diet in the Biebrza NP. $^{-1}$
[1]Shipley *et al.*, 1998; [2]Lundberg *et al*., 1990; [3]Cederlund & Nyström, 1981; [4]Hobbs *et al*., 1982; [5]Spalinger *et al.*, 2010; ' Mean value of sample material from April, June and August; " Mean value of sample material from April, May, July and October.

Tree species	Nitrogen (% dry mass)	Nitrogen ($g*kg^{-1}$ DM)	Phosphorus (% dry mass)	Digestibility (% dry mass)	Plant parts analysed	Ecosystem type	Region
Betula spp.	1.6 [3']		0.2 [3']	-	twigs (with leaves) [3]	Pine forest with shrubs [3]	Central Sweden [3]
Betula pubescens	1.1 (se = 0.02) [1]			32 (0.5) [1]	twigs (with leaves) [1]	Coastal forest [1]	Northern Sweden [1]
	0.99 (sd = 0.06) [2]			27 (sd = 1) [2]	twigs (with leaves) [2]	Young deciduous forest stand [2]	Northern Sweden [2]
Populus spp.	1.1 (se = 0.02) [1]			41 (0.2) [1]	twigs (with leaves) [1]	Coastal forest [1]	Northern Sweden [1]
Populus tremula	-	9 [4]			leaves [4]	upper montane part of the Rocky Mountain NP [4]	Colorado [4]
		16 [5]			leaves [5]	Boreal and arctic [5]	Alaska [5]
Salix caprea	1.0 (se = 0.03) [1]			42 (0.3) [1]	twigs (with leaves) [1]	Coastal forest [1]	Northern Sweden [1]
Salix spp.	1.1 (se = 0.02) [1]			43 (0.2) [1]	twigs (with leaves) [1]	Coastal forest [1]	Northern Sweden [1]
	1.32 [3"]		0.2 [3"]	-	twigs (with leaves) [3]	Pine forest with shrubs [3]	Central Sweden [3]
Sorbus aucuparia	0.9 (se = 0.00) [1]			37 (0.6) [1]	twigs (with leaves) [1]	Coastal forest [1]	Northern Sweden [1]
	1.01 (sd = 0.09) [2]			41 (sd = 4) [2]	twigs (with leaves) [2]	Young deciduous forest stand [2]	Northern Sweden [2]

C. Sedges, grasses and shrubs

Table III.19: Mean nutrient (N and P) content of sedges and reed. Nutrient content of grasses was not known. Data from Biebrza NP, 2010 (pers. inf. Bormans M., 2011).

Sedges and reed	N		P		Sample size
	µ	sd	µ	sd	
Carex appropinquata	10.22	1.20	1.50	0.35	8
Carex elata	9.55	1.96	0.88	0.20	11
Carex lasiocarpa	9.62	1.99	0.78	0.23	3
Carex nigra	8.55	0.87	1.27	0.27	3
Carex rostrata	10.27	-	2.35	-	1
Carex acuta	12.91	-	1.95	-	1
Phragmites australis	7.10	2.02	0.88	0.53	4
Sedges and reed	10.19	0.89	1.25	0.17	

D. Herbs

Table III.20: Mean nutrient (N and P) content of herbs. Data from Biebrza NP, 2010 (pers. inf. Bormans M., 2011).

Herbs	N		P		Sample size
	µ	sd	µ	sd	
Caltha palustris	12.59	4.43	2.17	0.74	5
Menyanthes trifoliata	18.94	6.64	2.70	0.94	10
Potentilla palustris	12.74	3.39	1.57	0.36	14
Equisetum fluviatile	10.27	0.60	1.90	1.38	4
Thelypteris palustris	14.98	3.47	1.68	0.73	7
Herbs	13.90	3.71	2.00	0.83	

APPENDIX IV: DIET PREFERENCES LINKED TO PLANT HEIGHT AND WATER LEVEL

+ Positively selected species

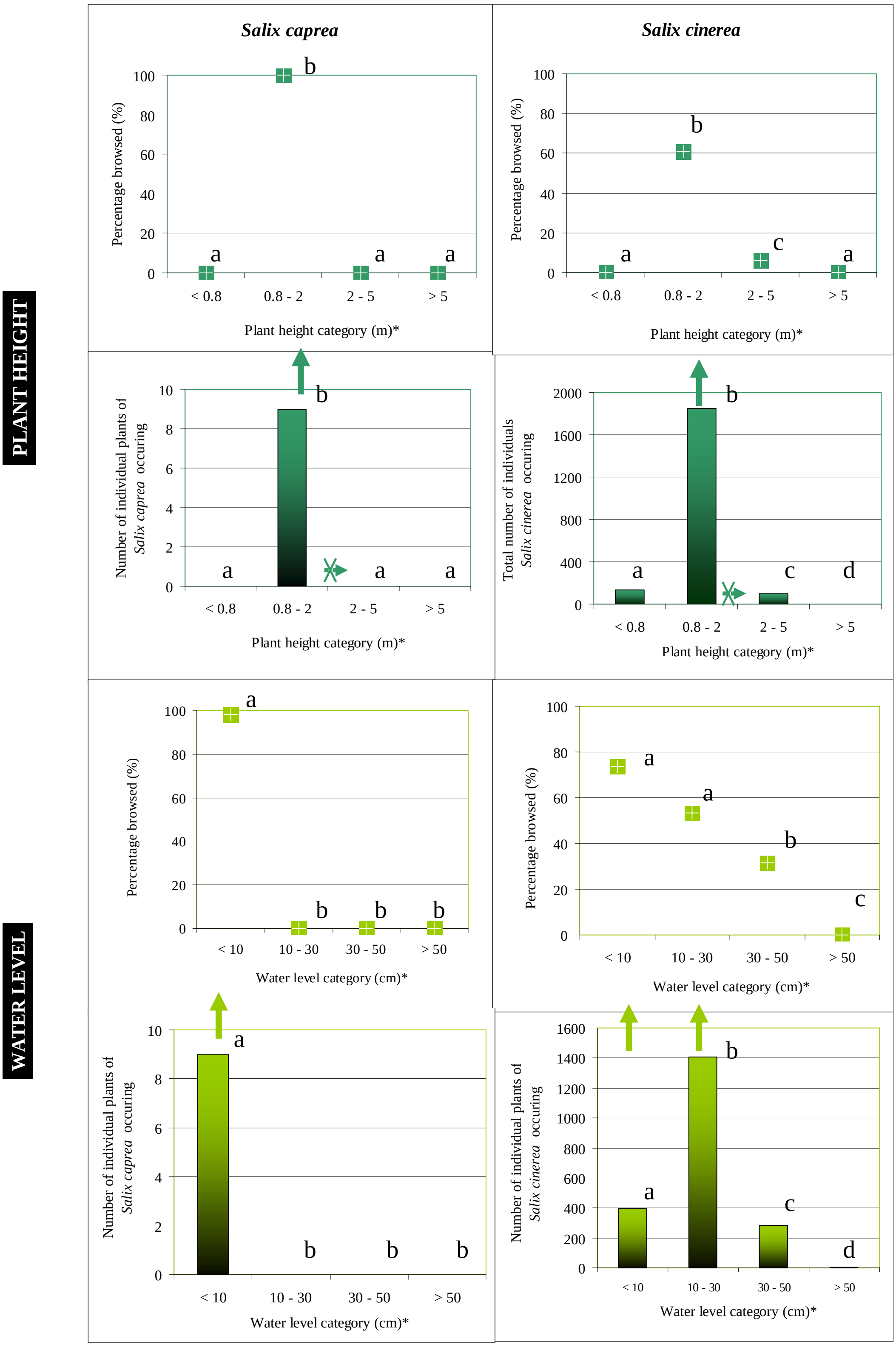


Fig. IV.36: Two species, positively selected by moose. Percentage browsed per plant height and per water level category is given and number of individuals per category occurring. Statistically significant differences ($p<0.05$) of frequencies between the categories are indicated by **different** letters.

- Negatively selected species

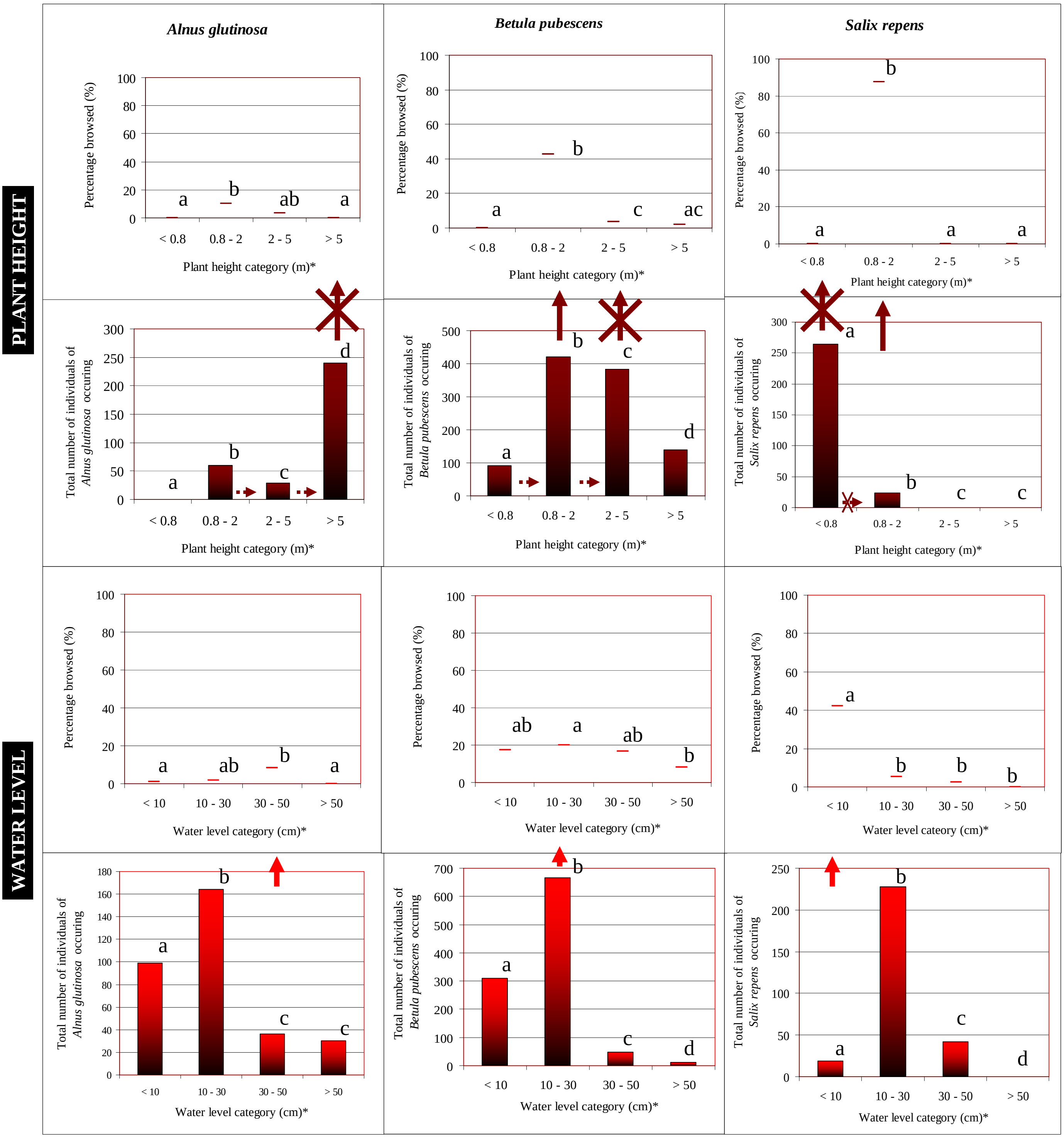


Fig. IV.37: Three species, negative selected by moose. Percentage browsed per plant height and per water level category is given and number of individuals per category occurring. Statistically significant differences (p<0.05) of frequencies between the categories are indicated by **different** letters.

APPENDIX V: STATISTICAL ANALYSIS OF FORAGE DIFFERENCES IN STRUCTURAL VEGETATION TYPES

Fig. 1.10

Table V.21: Differences between structural vegetation types (Fig.1.14).

Structural vegetation types	Coniferous forest	Brushwood	Brook forest	Reed marsh
Brushwood	0.99 ns			
Brook forest	0.35 ns	0.46 ns		
Reed marsh	0.25 ns	0.33 ns	0.99 ns	
Sedge marsh	0.23 ns	0.31 ns	0.99 ns	0.99 ns

Fig. 1.11 A

Table V.22: Over all structural vegetation types. Differences in preferences: there is a difference
(p= 0.009634 **, F-test= 6.0175, df= 3) (Fig. 1.15 over all). Winter needs to be excluded when looking at summer diet.

Plant categories	Conifers	Grasses, sedges and reed	Herbs
Deciduous trees	0.72 ns	< 0.05 *	< 0.05 *
Conifers		0.13 ns	0.14 ns
Grasses, sedges and reed			1.00 ns

Table V.23: Coniferous forest (p=0.0007824 ***, F-test= 9.5, df=3) (Fig. 1.11 A)

Plant categories	Conifers	Grasses, sedges and reed	Herbs
Deciduous trees	0.86 ns	< 0.01 **	< 0.01 **
Conifers		< 0.01 **	< 0.01 **
Grasses, sedges and reed			1.00 ns

Table V.24: Brushwood (p= < 2.2e-16 ***, F-test= 49.6, df=3) (Fig. 1.11 A).

Plant categories	Conifers	Grasses, sedges and reed	Herbs
Deciduous trees	< 0.001 ***	< 0.001 ***	< 0.001 ***
Conifers		1.00 ns	0.96 ns
Grasses, sedges and reed			0.94 ns

Table V.25: Brook forest (p= 0.016 *, F-test= 3.7, df=3) (Fig. 1.11 A).

Plant categories	Conifers	Grasses, sedges and reed	Herbs
Deciduous trees	< 0.01 **	0.20^{ns}	0.12^{ns}
Conifers		0.58^{ns}	0.72
Grasses, sedges and reed			1.00^{ns}

Table V.26: Reed marsh (p= 7.51e-05 ***, F-test= 9.5, df=3) (Fig. 1.11 A).

Plant categories	Conifers	Grasses, sedges and reed	Herbs
Deciduous trees	< 0.001 ***	< 0.001 ***	< 0.001 ***
Conifers		1.00^{ns}	1.00^{ns}
Grasses, sedges and reed			1.00^{ns}

Table V.27: Sedge marsh (p= 0.006082 **, F-test= 4.8, df=3) (Fig. 1.11 A).

Plant categories	Conifers	Grasses, sedges and reed	Herbs
Deciduous trees	< 0.05 *	< 0.05 *	< 0.05 *
Conifers		1.00^{ns}	1.00^{ns}
Grasses, sedges and reed			1.00^{ns}

Table V.28: Brushwood ($p < 2.2e-16$ *** , F-test= 9.50 df= 13) (Fig. 1.11 B2).

Plant categories	*Salix cinerea*	*Betula pubescens*	*Frangula alnus*	*Salix repens*	*Salix nigricans*	*Alnus glutinosa*	*Salix pentandra*	*Viburnum opulus*	*Populus tremula*	*Salix triandra*	*Corylus avellana*	*Salix caprea*	*Sorbus aucuparia*
Betula pubescens	0.42 ^{ns}												
Frangula alnus	0.99 ^{ns}	0.99 ^{ns}											
Salix repens	< 0.001 ***	0.14 ^{ns}	< 0.01 **										
Salix nigricans	< 0.01 **	0.98 ^{ns}	0.36 ^{ns}	0.94 ^{ns}									
Alnus glutinosa	< 0.001 ***	< 0.05 *	< 0.001 ***	1.00 ^{ns}	0.49 ^{ns}								
Salix pentandra	0.04 *	0.99 ^{ns}	0.68 ^{ns}	0.73 ^{ns}	1.00 ^{ns}	0.21 ^{ns}							
Viburnum opulus	< 0.001 ***	0.19 ^{ns}	< 0.01 **	1.00 ^{ns}	0.96 ^{ns}	1.00 ^{ns}	0.81 ^{ns}						
Populus tremula	< 0.001 ***	< 0.01 **	< 0.001 ***	1.00 ^{ns}	0.37 ^{ns}	1.00 ^{ns}	0.14 ^{ns}	1.00 ^{ns}					
Salix triandra	< 0.001 ***	0.18 ^{ns}	< 0.01 **	1.00 ^{ns}	0.96 ^{ns}	1.00 ^{ns}	0.78 ^{ns}	1.00 ^{ns}	1.00 ^{ns}				
Corylus avellana	< 0.001 ***	< 0.01 **	< 0.001 ***	1.00 ^{ns}	0.22 ^{ns}	1.00 ^{ns}	0.07 ^{ns}	0.99 ^{ns}	1.00 ^{ns}	0.99 ^{ns}			
Salix caprea	< 0.001 ***	< 0.05 *	< 0.001 ***	1.00 ^{ns}	0.55 ^{ns}	1.00 ^{ns}	0.07 ^{ns}	1.00 ^{ns}	1.00 ^{ns}	1.00 ^{ns}	1.00 ^{ns}		
Sorbus aucuparia	< 0.001 ***	< 0.01 **	< 0.001 ***	1.00 ^{ns}	0.22 ^{ns}	1.00 ^{ns}	0.07 ^{ns}	0.99 ^{ns}	1.00 ^{ns}	0.99 ^{ns}	1.00 ^{ns}	1.00 ^{ns}	

Table V.29: Brook forest (p = 0.01914, Kruskal-Wallis chi-squared = 19.8072, df = 9) (Fig. 1.11 B3).

Plant categories	*Frangula alnus*	*Alnus glutinosa*	*Salix cinerea*	*Betula pubescens*	*Corylus avellana*	*Sorbus aucuparia*	*Quercus robur*	*Tilia Platyphyllos*	*Ribes nigrum*
Alnus glutinosa	< 0.05 *								
Salix cinerea	0.25 ^{ns}	0.50 ^{ns}							
Betula pubescens	< 0.05 *	0.90 ^{ns}	0.53 ^{ns}						
Corylus avellana	0.25 ^{ns}	0.50 ^{ns}	1.00 ^{ns}	0.53 ^{ns}					
Sorbus aucuparia	0.14 ^{ns}	0.84 ^{ns}	0.77 ^{ns}	0.84 ^{ns}	0.73 ^{ns}				
Quercus robur	< 0.05 *	0.36 ^{ns}	0.19 ^{ns}	0.36 ^{ns}	0.18 ^{ns}	0.32 ^{ns}			
Tilia Platyphyllos	< 0.01 **	0.36 ^{ns}	0.15 ^{ns}	0.36 ^{ns}	0.15 ^{ns}	0.30 ^{ns}	1.00 ^{ns}		
Ribes nigrum	< 0.05 *	0.36 ^{ns}	0.19 ^{ns}	0.36 ^{ns}	0.18 ^{ns}	0.32 ^{ns}	1.00 ^{ns}	1.00 ^{ns}	
Salix pentandra	< 0.01 **	0.08 ^{ns}	< 0.05 *	0.08 ^{ns}	< 0.05 *	0.08 ^{ns}	0.35 ^{ns}	0.35 ^{ns}	0.35 ^{ns}

Table V.30: Reed marsh (p = 0.003, Kruskal-Wallis chi-squared = 19.5, df = 6) (Fig. 1.11 B4).

Plant categories	*Salix cinerea*	*Betula pubescens*	*Salix repens*	*Betula humilis*	*Ribes nigrum*	*Salix pentandra*
Betula pubescens	0.10 ^{ns}					
Salix repens	0.30 ^{ns}	0.59 ^{ns}				
Betula humilis	< 0.05 *	0.66 ^{ns}	0.28 ^{ns}			
Ribes nigrum	< 0.01 **	0.17 ^{ns}	0.08 ^{ns}	0.36 ^{ns}		
Salix pentandra	< 0.01 **	0.17 ^{ns}	0.08 ^{ns}	0.36 ^{ns}	-	
Frangula alnus	< 0.01 **	0.17 ^{ns}	0.08 ^{ns}	0.36 ^{ns}	-	-

Table V.31: Sedge marsh (p = 0.2194, F-test = 1.45, df = 5) (Fig. 1.11 B5).

Plant categories	*Salix cinerea*	*Betula pubescens*	*Salix repens*	*Salix pentandra*	*Alnus glutinosa*
Betula pubescens	0.75 ^{ns}				
Salix repens	0.84 ^{ns}	1.00 ^{ns}			
Salix pentandra	1.00 ^{ns}	0.61 ^{ns}	0.71 ^{ns}		
Alnus glutinosa	0.54 ^{ns}	1.00 ^{ns}	1.00 ^{ns}	0.40 ^{ns}	
Salix nigricans	1.00 ^{ns}	1.00 ^{ns}	1.00 ^{ns}	0.40 ^{ns}	1.00 ^{ns}

Fig. 1.16 Brushwood: connected versus islands: there is no difference between brushwood connected to forest and islands (p = 0.53, F-test = 0.40, df = 1)

Table V.32: Brushwood: connected to forest (p = 0.007163 **, F-test = 3.01, df = 8) (Fig. 1.12 B1).

Plant categories	*Salix cinerea*	*Betula pubescens*	*Salix nigricans*	*Salix pentandra*	*Alnus gutinosa*	*Salix repens*	*Frangula alnus*	*Corylus avellana*
Betula pubescens	0.17 ns							
Salix nigricans	0.57 ns	1.00 ns						
Salix pentandra	0.42 ns	1.00 ns	1.00 ns					
Alnus gutinosa	< 0.05 *	0.98 ns	0.73 ns	0.85 ns				
Salix repens	< 0.05 *	0.98 ns	0.73 ns	0.85 ns	1.00 ns			
Frangula alnus	< 0.05 *	0.98 ns	0.73 ns	0.85 ns	1.00 ns	1.00 ns		
Corylus avellana	< 0.05 *	0.98 ns	0.73 ns	0.85 ns	1.00 ns	1.00 ns	1.00 ns	
Salix triandra	0.13 ns	1.00 ns	0.99 ns	1.00 ns	0.99 ns	0.99 ns	0.99 ns	0.99 ns

Table V.33: Brushwood: connected to forest (p = 0.51, F-test = 0.86, df = 4) (Fig. 1.12 B2).

Plant categories	*Salix cinerea*	*Betula pubescens*	*Salix nigricans*	*Salix pentandra*	*Alnus gutinosa*	*Salix repens*	*Frangula alnus*	*Corylus avellana*
Betula pubescens	0.17 ns							
Salix nigricans	0.57 ns	1.00 ns						
Salix pentandra	0.42 ns	1.00 ns	1.00 ns					
Alnus gutinosa	< 0.05 *	0.98 ns	0.73 ns	0.85 ns				
Salix repens	< 0.05 *	0.98 ns	0.73 ns	0.85 ns	1.00 ns			
Frangula alnus	< 0.05 *	0.98 ns	0.73 ns	0.85 ns	1.00 ns	1.00 ns		
Corylus avellana	< 0.05 *	0.98 ns	0.73 ns	0.85 ns	1.00 ns	1.00 ns	1.00 ns	
Salix triandra	0.13 ns	1.00 ns	0.99 ns	1.00 ns	0.99 ns	0.99 ns	0.99 ns	0.99 ns

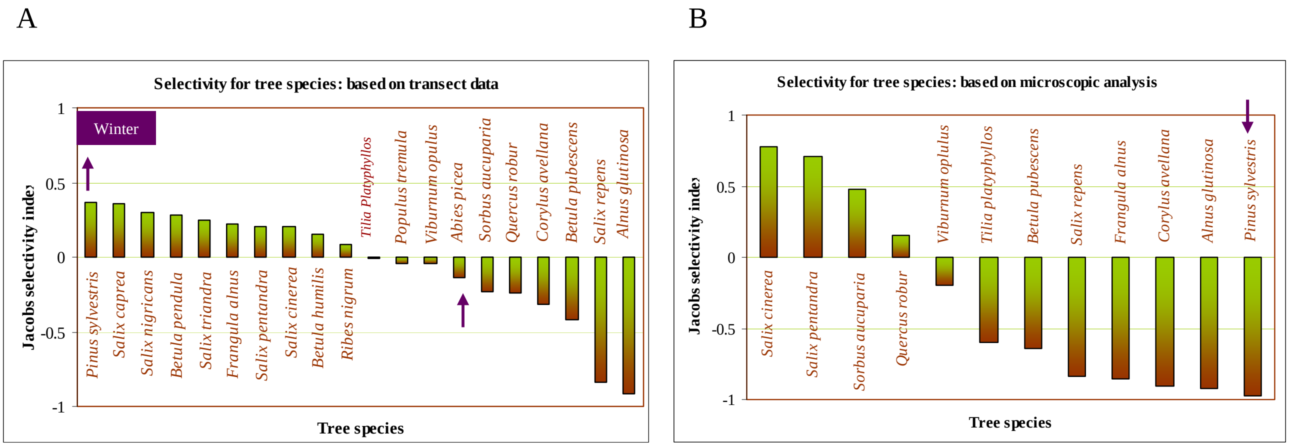
APPENDIX VI: TABLE ON THE DIET OF MOOSE

Table VI.34: The main browse species for certain studies are listed per season. The table shows that species contributing to the diet differ between ecosystem types and regions. Though some species (*Betula* spp.and *Salix* spp.) seem to contribute to the diet in many regions. Letters: order of most contributing to the diet (a > b > c > d).

Reference	Plant species	% of the diet	Season	Ecosystem type	Region	Data collection
Hörnberg, 2001	*Salix* spp.	40	year round	Forest	Sweden (5 sites spread over whole Sweden)	1969-1972
	Betula spp.	22				
	Pinus spp.	18				
	Juniperus spp.	10				
	Sorbus aucuparia	9				
	Populus spp.	8				
Broman *et al.*, 2003	*Betula pubescens*, *B. pendula* and *B. nana*	40 - 68	early summer	Forest	Sweden (6 sites spread over whole Sweden)	1991 - 2001
	Vaccinium myrtillus/V. vitis-idea	16 - 34				
Bjerga & Mysterud, 1999	*Betula pubescens*	a	summer	Forest on acid bedrock (boreal)	Southern Norway	1995
	Vaccinium myrtillus	b				
	Narthecium ossifragum	c				
Dungan & Wright, 2005	*Salix* spp.	80	summer	Riparian meadows Rocky Mountain NP	North-central Colorado	
	Carex spp.	12				
Edenius *et al.*, 2002	*Populus* spp.	a	late summer	Managed forest, mires and lakes	North Sweden	1998
	Sorbus aucuparia	b				
	Salix spp.	c				
	Betula pubescens	d				
Bergström & Hjeljord, 1987 in Danell *et al.*, 1994	*Pinus sylvestris*	-	winter	Forest	Sweden	- (1987)
	Betula pendula	-				
	Betula pubescens	-				
	Sorbus aucuparia	-				
	Populus tremula	-				
Shipley *et al.*, 1998	*Pinus sylvestris*	-	winter	Forest	North Sweden	1995
	Salix spp.	-				
Routledge & Roese, 2004	*Acer* spp.	a	winter	Coniferous-deciduous forest	Ontario (Canada)	1995
	Abies balsamea	b				
	Betula alleghaniensis	c				

APPENDIX VII: WINTER DIET OF MOOSE

The influence of moose on nutrient dynamics in winter, was beyond the scope of this study. Yet, few data were collected to assess whether winter activity of moose may overlap with summer patterns or not. By counting pellets on transects, I found that old pellets were concentrated in the coniferous forest (µ = 882 sd = 551 pellet heaps*ha^{-1}*month^{-1}) (df = 4, F = 21.3, p = 1.8e-11 ***), whereas few were found in the brushwood (µ = 58 sd = 100 pellet heaps*ha^{-1}*month^{-1}). They occurred although not significantly more than in the brook forest, reed and sedge marsh. These findings correspond to Fedyk *et al.* (1984), who state that winter habitat for moose in the BNP comprises pine forests, including clearings and young pine plantations and willow and birch stands. This suggests, that nutrient input in winter, does not show the same pattern as in summer. Concerning nutrient removal, Borowska & Konopko (1994) found that the browsing of willow-birch shrubs was high in BNP. Moreover, they state that moose not only browsed the last year's growth of shoots but also bark and twigs from earlier years. Several authors confirm that conifers may be a main browse species in winter (Danell *et al.*, 1994; Shipley *et al.*, 1998; Klosowscy *et al.*, 2009). Danell *et al.* (1994), however, state that conifers are not preferred, but still consumed, as they are often available in a large proportion. By contrast, the transect data of this study showed a preference for *Pinus sylvestris*, being a winter preference, yet *Abies picea*, seemed to be slightly avoided (Fig)



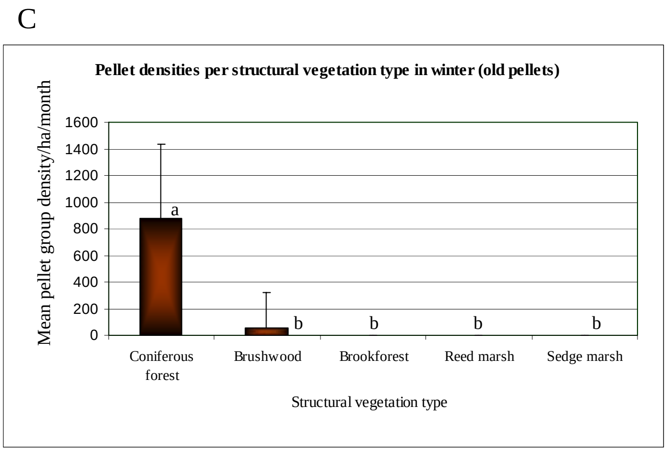


Fig. VII.38 A and B: Jacobs selectivity index, A: based on transect data, B: right based on microscopic data. C: Pellet density (of old pellets) per structural vegetation type, based on counting pellets on transects.

APPENDIX VIII: CALCULATION OF THE YEARLY NUTRIENT UPTAKE BY EXISTING VEGETATION

Concept of "mean theoretical shrubs"

Mean theoretical shrubs were made, based on mean values of parameters of sampled shrubs in the field. Only shrubs of 4, 5, 6 and 8 years old were sampled, so only from these I know a mean number of branches per shrub. But the estimated number of branches for a shrub of 8 years old was very low and only based on one measurement therefore the age category of 8 years old was not included.
Age category is used as a shrub from e.g. 4 years old, may be also slightly younger, which is between 3 and 4 years old.
Twig was used to determine the different woody parts belonging to different age categories of a *branch.*

Step 1: Over 12 sampled shrubs, the mean and standard deviation of N content (g nutrient*kg^{-1} DM) and P content (g nutrient*kg^{-1} DM) per twig age category (a) and for all leaves (b) was calculated.
The shrubs, sampled from different sites were used as repetition.

Per twig

Step 2: (nutrient content/1000) (g*g^{-1}) * dry mass per age category (g). This results in nutrient content (g) per age category *per twig.*

Table VIII.35: **Twigs**: mean nutrient content (g*kg^{-1} DM) (step 1) and nutrient content per *twig* (step 2); µ = mean and sd = standard deviation).

Step 1a							Step 2	
Age category	N (g/kg)		P (g/kg)		dry weight (g)		N (g) per branch	P (g) per branch
	µ	sd	µ	sd	µ	sd	N (g) *dry weight	P (g) *dry weight
1	9.815	2.015	1.467	0.252	11.636	3.185	0.114	0.017
2	6.733	0.977	0.825	0.156	7.700	6.910	0.052	0.006
3	5.960	1.527	0.740	0.185	23.071	8.995	0.138	0.017
4	4.805	1.368	0.597	0.163	25.508	10.913	0.123	0.015
5	5.569	1.401	0.606	0.145	24.956	16.569	0.139	0.015
6	5.388	1.332	0.517	0.121	12.300	7.174	0.066	0.006
7	5.066	1.362	0.437	0.078	11.025	3.475	0.056	0.005
8	6.622	0.050	0.563	0.072	28.450	0.450	0.188	0.016

Table VIII.36: **Leaves**: mean nutrient content (g per kg DM) (step 1) and nutrient content per *twig* (step 2) ; µ = mean and sd = standard deviation).

Step 2a							Step 3a
N (g*kg^{-1})		P (g*kg^{-1})		Age category	dry weight (g)	N (g) per branch	P (g) per branch
µ	sd	µ	sd			N (g) *dry weight	P (g) *dry weight
20.83871241	2.965721413	2.098142555	0.355342869	4	25.283	0.527	0.053
				5	24.113	0.502	0.051
				6	35.125	0.732	0.074

A. Minimum estimation of yearly nutrient uptake

This estimation assumes that *all* the nutrients of the leaves are retreated and allocated in the shrub before the leaves fall. This means shrubs only take up nutrients for primary and secondary growth of twigs.

Per branch

Step 3a: Calculate nutrient content per branch (twigs accumulated and leaves) for age category 4, 5 and 6.
e.g. N content per brancfor age category 4:
N (g) per branch $_{1yeartwig}$ + N (g) per branch$_{2yeartwig}$ + N (g) per branch$_{3yeartwig}$ + N (g) per branch$_{4yeartwig}$ + N (g) per branch$_{4yearleaves}$

Table VIII.37a: Nutrient content of a *branch.*

Age category	Accumulated N (g)	Accumulated P (g)
4	0.95	0.11
5	1.07	0.12
6	1.36	0.15

Per shrub

Step 4a: Calculate the nutrient content of a *shrub*, nutrient content *per branch* (g) * mean number of branches of the age category

Table VIII.38a: Nutrient content of a *shrub.*

Age category	Mean number of branches	N (g) per branch * number of branches	P (g) per branch * number of branches
4	9.667	9.212	1.051
5	10.750	11.477	1.305
6	11.500	15.678	1.735

Step 5a: Nutrient uptake per year: differences between shrubs (6-5 and 5-4)

Table VIII.39a: Nutrient uptake per year (summer).

Age category	diff N ($g*yr^{-1}$)	diff P ($g*yr^{-1}$)
5 - 4	2.264	0.254
6 - 5	4.202	0.430

Per hectare of willow shrubs

For a willow cover of 100%, 30223 willows*ha^{-1} were counted

Step 6a: Proportion of cover * mean number of willows that cover 100%*ha^{-1}

Step 7a: Nutrient uptake per year (g*yr^{-1}) * mean number of willows*ha^{-1}

Step 8a: Nutrient uptake/1000 (kg*ha*yr^{-1})

Table VIII.40a: Yearly nutrient uptake for a large scale willow patch; µ = mean and sd = standard deviation.

Large scale willow patch		Step 6a	Step 7a		Step 8a	
Cover (%)		number of willows per ha	N	P	N	P
µ	sd		kg*ha*yr^{-1}	kg*ha*yr^{-1}	kg*ha*yr^{-1}	kg*ha*yr^{-1}
68	11	20552	46531	5220	**47**	**5**
			86355	8835	86	9

Table VIII.41a: Yearly nutrient uptake for small scale willow patches; µ = mean and sd = standard deviation.

Small scale willow patches		Step 6a	Step 7a		Step 8a	
Cover (%)		number of willows per ha	N	P	N	P
µ	sd		g/ha/yr	g/ha/yr	kg/ha/yr	kg/ha/yr
33	7	9974	22581	2533	**23**	**3**
			41907	4288	42	4

B. Maximum estimation of yearly nutrient uptake

This estimation assumes that *no* nutrients of leaves are retreated before the leaves fall. This means shrubs take up nutrients for primary and secondary growth of twigs and for leaves.

Per branch

<u>Step 3b</u>: Calculate nutrient content per branch (twigs accumulated *without* leaves) for age category 4, 5 and 6.
e.g. N content per brancfor age category 4:
N (g) per branch $_{\text{1yeartwig}}$ + N (g) per branch$_{\text{2yeartwig}}$ + N (g) per branch$_{\text{3yeartwig}}$ + N (g) per branch$_{\text{4yeartwig}}$ ~~+ N (g) per branch$_{\text{4yearleaves}}$~~

Table VIII.42b: Nutrient content of a *branch.*

Age category	Accumulated N (g)	Accumulated P (g)
4	0.4261	0.0557
5	0.5651	0.0708
6	0.6314	0.0772

Per shrub

<u>Step 4b</u>: Calculate the nutrient content of a *shrub*, nutrient content *per branch* (g) * mean number of branches of the age category

Table VIII.43b: Nutrient content of a *shrub.*

Age category	mean number of branches	N (g) per branch * number of branches	P (g) per branch * number of branches
4	9.667	4.119	0.539
5	10.750	6.075	0.762
6	11.500	7.261	0.888

<u>Step 5b</u>: Nutrient uptake per year: differences between shrubs (6 (with leaves) - 5 (without leaves) and 5 (with leaves) - 4 (without leaves))

Table VIII.44b: Nutrient uptake per year (summer).

Age category	diff N ($g*yr^{-1}$)	diff P ($g*yr^{-1}$)
5 (with leaves) - 4	7.357	0.767
6 (with leaves) - 5	9.603	0.974

Per hectare of willow shrubs

For a willow cover of 100%, 30223 willows/ ha were counted

Step 6b: Proportion of cover * mean number of willows that cover 100%/ha

Step 7b: Nutrient uptake per year (g*yr^{-1}) * mean number of willows*ha^{-1}

Step 8b: Nutrient uptake/1000 (kg*ha^{-1}*yr^{-1})

Table VIII.45b: Yearly nutrient uptake for a large scale willow patch.

Large scale willow shrubs		Step 6a	Step 7a		Step 8a	
Cover (%)		number of willows per ha	N	P	N	P
µ	sd		g*ha^{-1}*yr^{-1}	g*ha^{-1}*yr^{-1}	kg*ha^{-1}*yr^{-1}	kg*ha^{-1}*yr^{-1}
68	11	20552	151203	15759	**151**	**16**
			197366	20013	197	20

Table VIII.46b: Yearly nutrient uptake for a large scale willow patch.

Small scale willow patches		Step 6a	Step 7a		Step 8a	
Cover (%)		number of willows per ha	N	P	N	P
µ	sd		g*ha^{-1}*yr^{-1}	g*ha^{-1}*yr^{-1}	kg*ha^{-1}*yr^{-1}	kg*ha^{-1}*yr^{-1}
33	7	9974	73378	7648	**73**	**8**
			95781	9712	96	10

APPENDIX IX: SHRUB ENCROACHMENT IN BNP

Since 1900, shrub encroachment has advanced with approximately 300ha*yr^{-1} in BNP, endangering species rich open fen (Schmidt *et al.*, 2000). In 2000, approximately 18% of BNP consisted of shrubs, which is far more than it is used to be (Schmidt *et al.*, 2000). This stems from a change in the proportion of the vegetation zones (§ study site; § methods 1.2.2) occurring in BNP over time (Fig. IX.42). A main cause of this secondary succession is the cessation of the agricultural management. Due to agricultural activities, the landscape has changed to a more open fen area between 1700 and 1970 (Fig. V.3 right) (Klosowscy *et al.*, 2009). During this time, inhabitants of the area were farmers and lived from raw materials, collected in and around BNP (Klosowscy *et al.*, 2009). The fen meadows were mown in summer (Fig. IX.41) to make hay stacks, transported in winter when the meadows were more accessible (Klosowscy *et al.*, 2009). During this season, reed was cut as well to isolate houses and stables (Fig. IX.40 right) (Klosowscy *et al.*, 2009) and osiers were cut from willow shrubs to weave barriers between the fields and around the houses (Fig. IX.40 left) (Klosowscy *et al.*, 2009). Besides, peat was dug for fuel, which caused disturbed patches in the fen area (Fig. IX.41 right) (Klosowscy *et al.*, 2009).

Since 2005 (pers. inf. board BNP, 2010), mowing has started in BNP with “pistenbullies” (Fig. IX.43) and shrubs were chopped to recreate, partly, an open species rich fen.

Besides, by cessation of agricultural activities, shrub encroachment is enhanced by several factors, shown in Fig. IX.39.

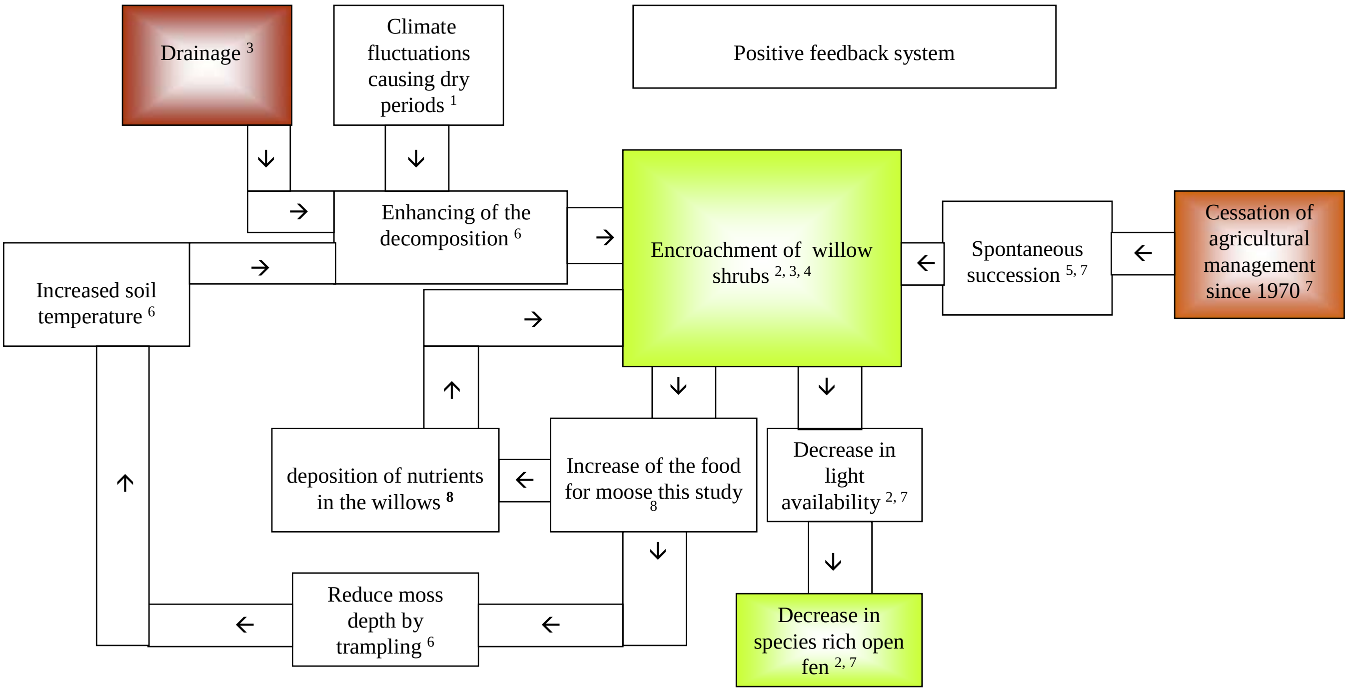


Fig. IX.39: Positive feedback system. In brown: the main causes; in green: the main effects. [1] Alm *et al.*, 1999; [2] Schmidt *et al.*, 2000; [3] Bokdam *et al.*, 2002; [4] Kotowski & Piórkowski, 2003; [5] De Fré & Hoffman, 2004; [6] Van der Wal & Brooker, 2004; [7] Klosowscy *et al.*, 2009; [8] suggested by this study.

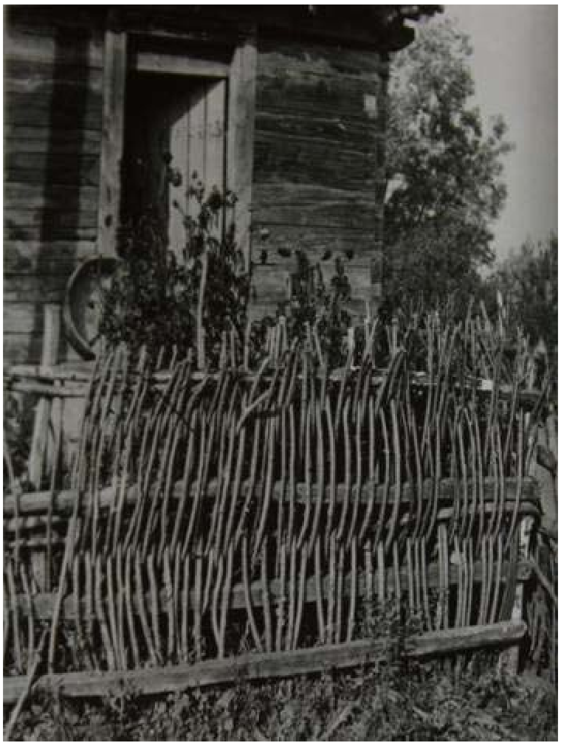


Fig. IX.40 Left: Osiers used to make barriers around houses and between fields. Right: In winter reed used to be cut to isolate houses (1700-1970) (photo’s: Klosowscy *et al.*, 2009).

Fig. IX.41 Left: Fields were mown, haystacks were made and transported as hay for the livestock during winter. Right: peat was dug to use as fuel (1700-1970) (photo’s: Klosowscy *et al.*, 2009).

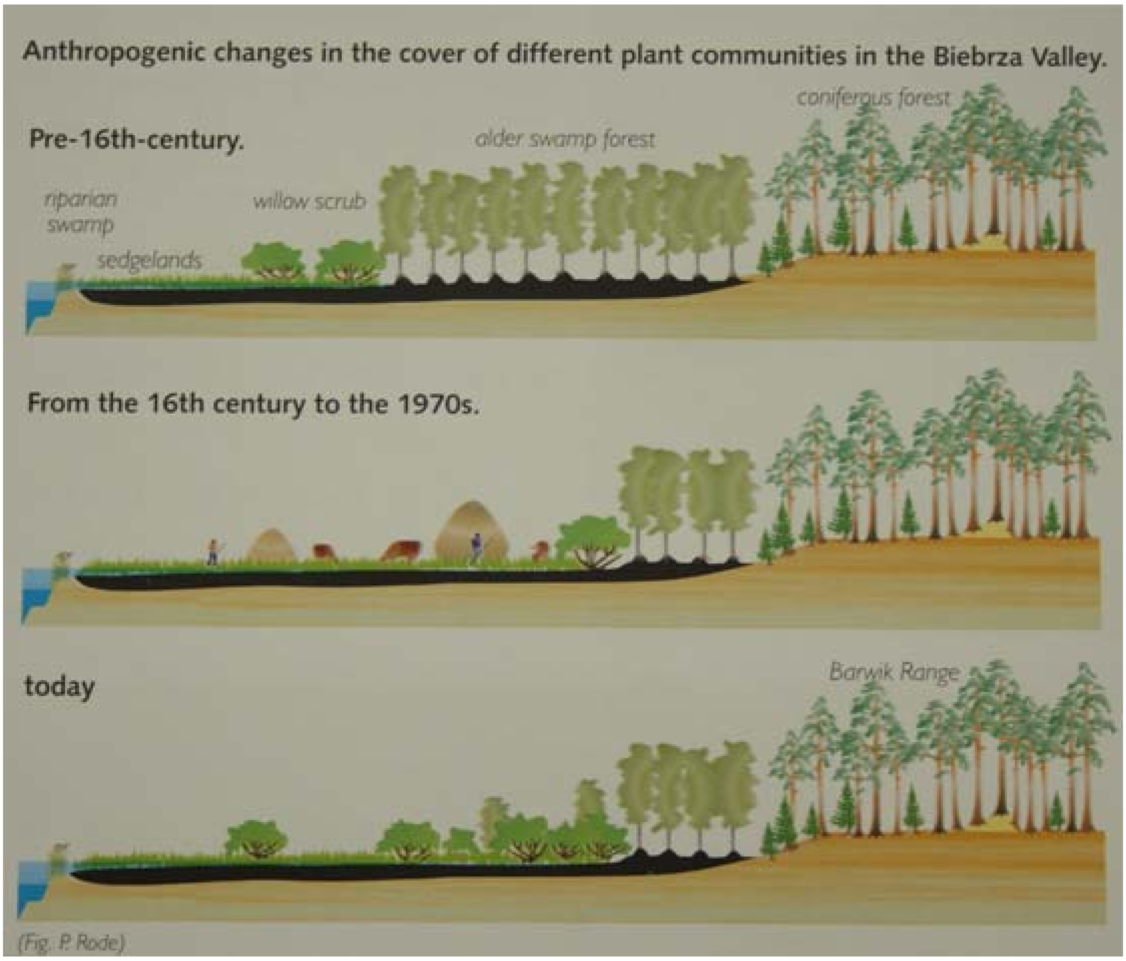


Fig. IX.42: The evolution of the landscape of the BNP (1700-1970) (Illustration: Klosowscy *et al.*, 2009).

Fig. IX.43: Recent mow management, using ‘Pistenbullies’ (photo: 2010).

APPENDIX II: REFERENCE COLLECTION FOR THE MICROSCOPIC DIET ANALYSIS

Photographs are made from microscopic slides of plant epidermises, collected in the Biebrza National Park, by an Olympus BX50 C-4040 zoom, F 1.8. Except for the photographs of mosses and veins which are made by a CANON EOS 1000D, EFS 18-55mm zoom. Photographs of veins were made from pellet samples, but the structures were compared with examples from the microscopic slides of plant epidermises of leaves collected in the Biebrza National Park. Samples of mosses were collected in Belgium.

The photo of *Alnus glutinosa* originates from the eference collection of Hofman Emilia (pers. inf., 2010) from plant samples collected in the Białowieża National Park.

1. Characteristics

- **Cell form, size and length in particular** is given when it is an important characteristic to distinguish between similar looking cells of other species
- **Form, size and density stomata**
- **Number of cells around the stomata**
- **Other peculiarities**

2. Classification

I Monocotyledons

Monocotyledons have very well structured and rather uniform, mostly rectangular cells, ordered like bricks in rows. These characteristics make them be easily distinguished from dicotyledons. The stomata as well look slightly different from those of dicotyledons.
In order with the most confusable species compared.

PLANT CATEGORY: GRASSES, SEDGES AND REED*

*Rushes are included, but not mentioned in the plant category as they are of minor importance for the moose diet

I.a Sedges, grasses, reed and rushes (Ordo *Poales*)………… ……………………………p.92

Tall *Carex spp.*
Small *Carex spp.*
Phragmites australis
Poaceae
Typha latifolia
Juncaceae

PLANT CATEGORY: CONIFERS (with deciduous shrubs = WOOD)

II Gymnosperm trees……………………………………………………………………...p.96

Cells look similar to those of monocotyledons but they are less structured.

Abies picea
Pinus sylvestris

III Dicotyledons

Considering the tree species in this collection, it is able to distinguish two groups based on two kinds of cells: “sharp-edged cells” and “cells with rounded corners”. In contrast to the cells in rows of monocotyledons, those of dicotyledons have a variable number of corners and rather a different cell size. Despite this variation cells might look quite rigid.

PLANT CATEGORY: DECIDUOUS SHRUBS (with conifers = WOOD)

III.a1 Trees – sharp-edged cells…………………………………………………………..p.100

Betula pubescens
Salix repens
Salix cinerea
Salix pentandra
Sorbus aucuparia
Quercus robur

III.a2 Trees – cells with rounded corners (puzzled form)……………………………....p.103

Alnus glutinosa
Corylus avellana
Frangula alnus
Tilia platyphyllos
Viburnum opulus

Twigs

PLANT CATEGORY: HERBS

III. b Herbs………………………………………………………………………………….p.97

The herbs in this collection have in general larger cells and stomata then those of trees. Cells are also less rigid than those of trees, they are rather bloated. It might be caused by the fact that many herbs in this collection are adapted to marshes are even to open water.

Nuphar luteus
Potentilla palustris
Menyanthes trifoliata
Eupatorium cannabinum
Caltha palustris
Vaccinium myrtillus
Hydrocharis morsus-ranae
Ceratophyllaceae

IV *Pteridophyta*………………………………………………………………………...p.103

Equisetum arvense
Thelypteris palustris

PLANT CATEGORY: MOSSES

Mosses are recognisable as they have tiny, squared or round cells in rows.

Veins are very tough, fibrous, chequered structures. Dark brown veins, of which the fibrous pattern is barely recognisable, are parts of tree species (twigs in Table 1.2), lighter variants may be part of any of the plant categories. Often curls (fibres) are visible.

COMMENT

When not a specific species, but a family, genus or even class is tried to be comprised with cell and stomata characteristics, a representative part of species belonging to those were sampled and/or it was checked if they were representative by comparing them with the extended and precise reference collection of Emilia Hofman (pers. inf., 2010), from samples collected in the Białowieża National Park. When it was possible, the comparison was also done for the species described.

I Monocotyledons

I.a Sedges, grasses, reed and rushes (Ordo *Poales)*

Tall *Carex spp.*, family *Cyperaceae*

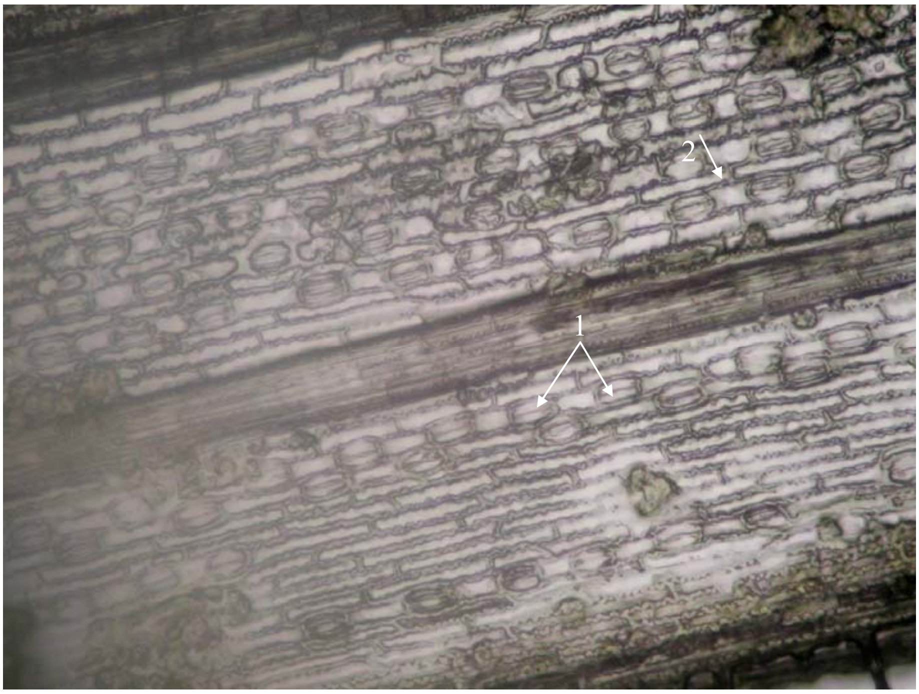


Photo X.44: Carex species have the most uniform and ordered cells (2) of all monocotyledons I looked at. Large Carex species have large cells (+/- 100µm long). Milled edges like telephone lines and rather squared cells alternating with stomata or long rigid cells (also along the veins). Stomata are large and occur in large quantities (1).

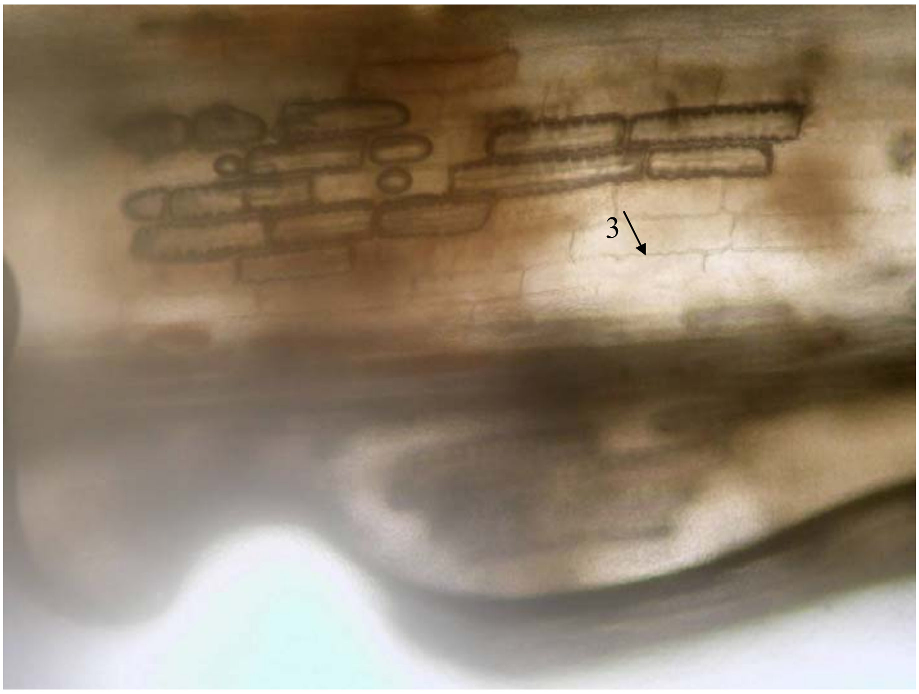


Photo X.45: Cell walls may be thin (3) (in contrast to the previous photo), but are still rigid and very ordered.

Small *Carex spp.*, family *Cyperaceae*

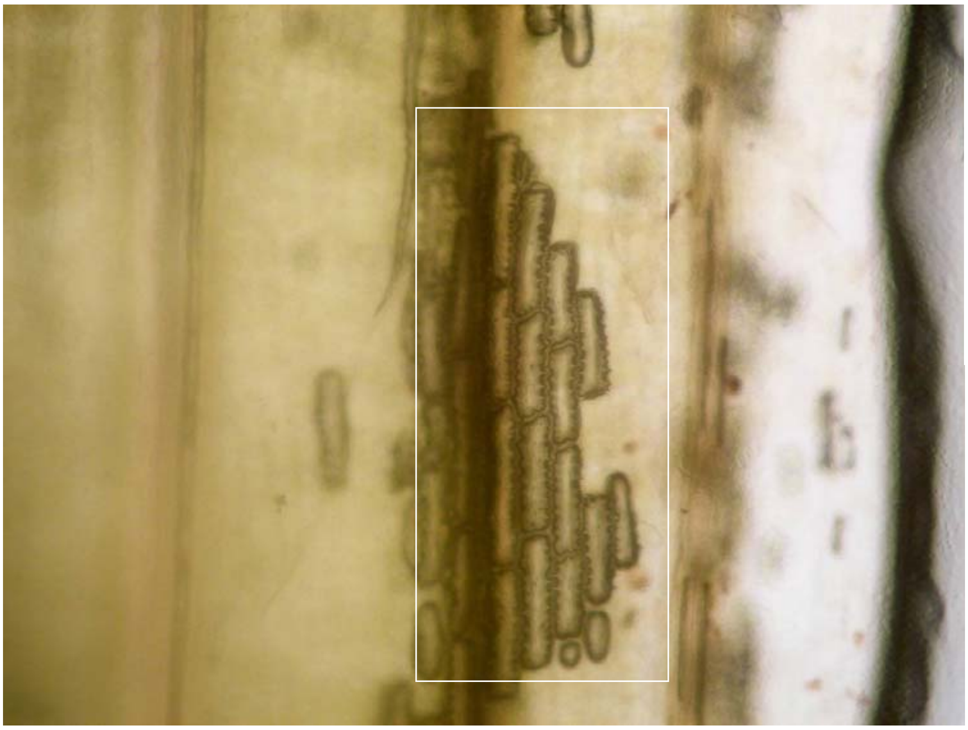


Photo X.46: Cells are narrower and less long (+/- 50µm long) than the tall *Carex* species.

Phragmites australis, genus: *Phragmites*, family *Poaceae*

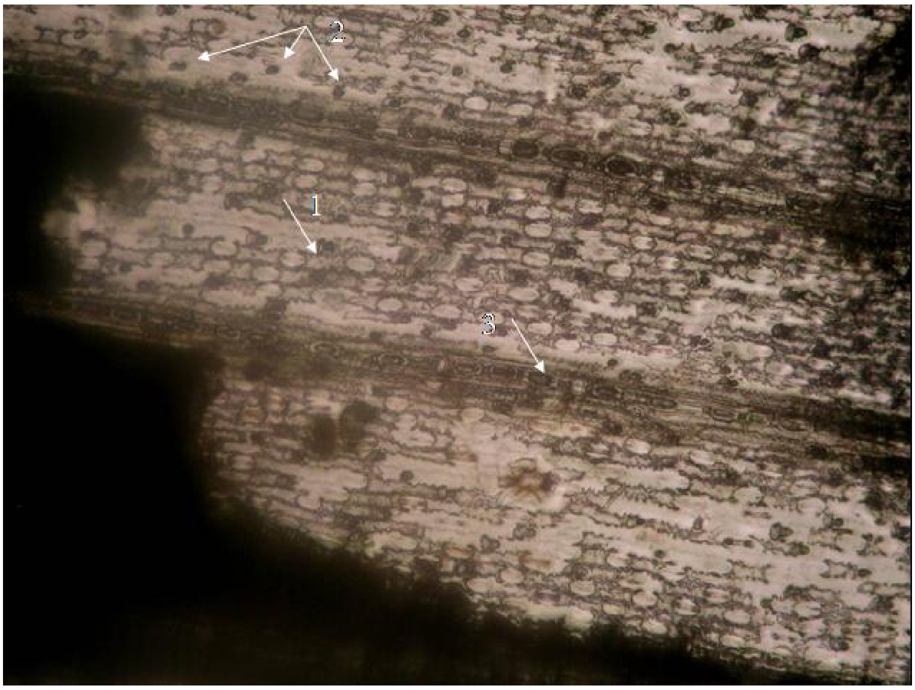


Photo: X.47: Cells are less long than *Carex* species (1). Stomata remnants as black small structures, are a very recognisable character (3).

Poaceae (family of the true grasses) (except for the genus *Phragmites)*

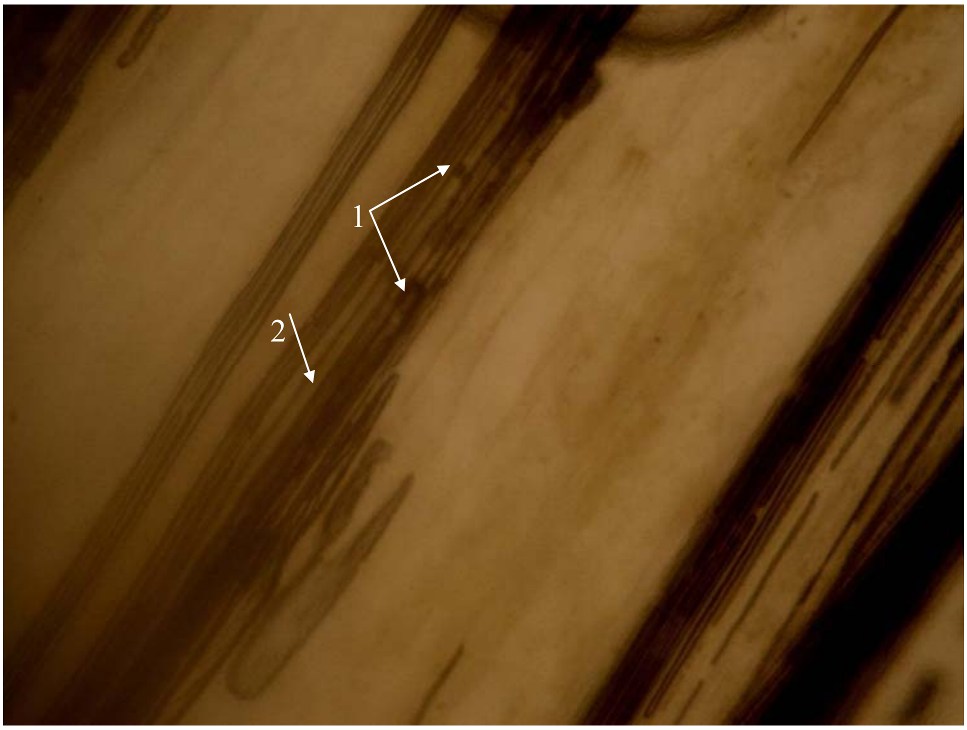


Photo X.48: An important characteristic of grasses are the dark ‘dividing walls’ in between the cells (1). Cells are mostly very elongated with varying width and length (2).

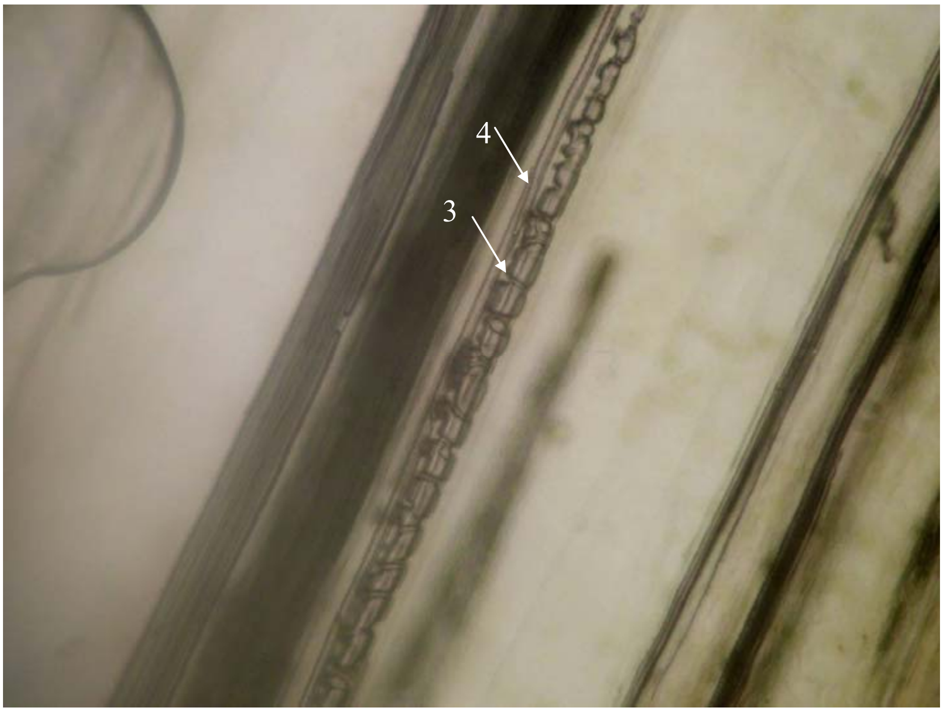


Photo X.49: Sometimes smaller cells occur with irregular shape and length (3), alternated by rigid cell lines (4).

Typha latifolia, family *Typhaceae*

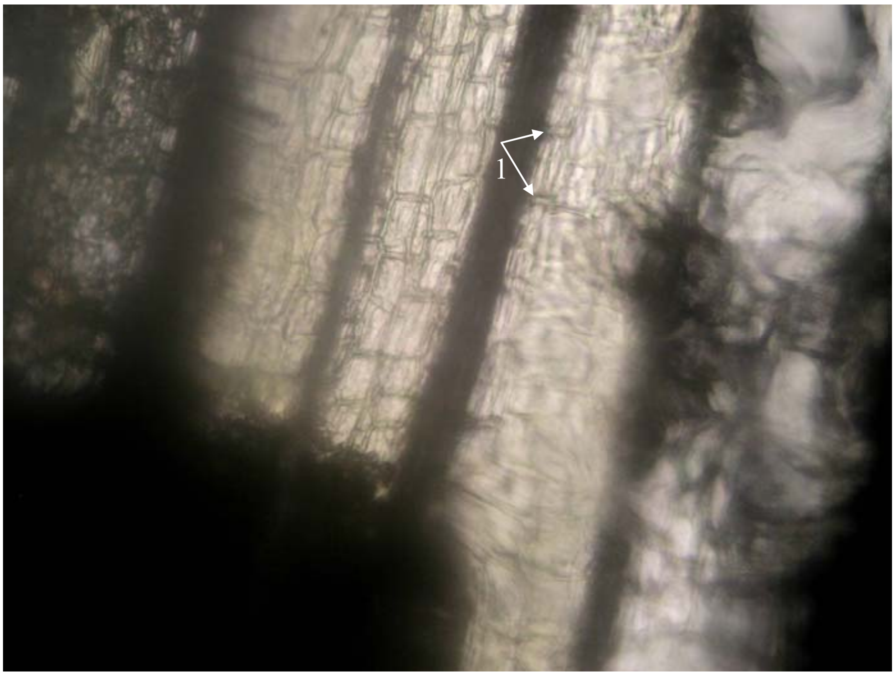


Photo X.50: *Typha latifolia* has rather squared cells with ‘dividing walls’ in between the cells (1) and has very few stomata.

Juncaceae (the rush family)

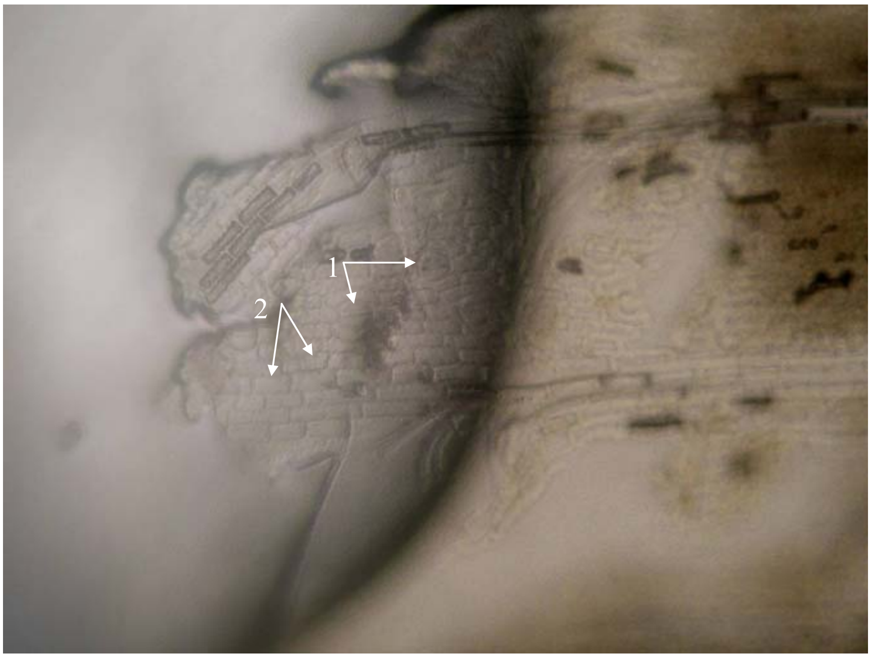


Photo X.51: Stomata are very round (1). Cells are small and structured, but seem to be mouldable (2).

II Gymnosperm trees

Abies picea

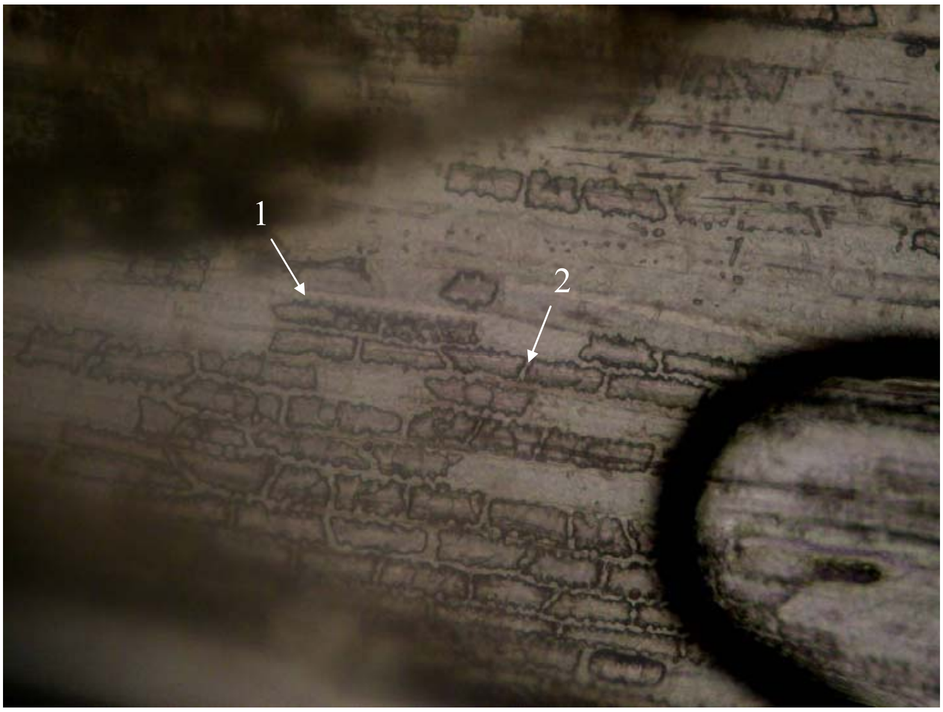


Photo X.52: Cells have milled edges (1). When zooming in and out the edges look like pearls on a chain. The intercellular space is larger than those of *Carex* spp. as *Abies picea* has more irregular cells (2).

Pinus sylvestris

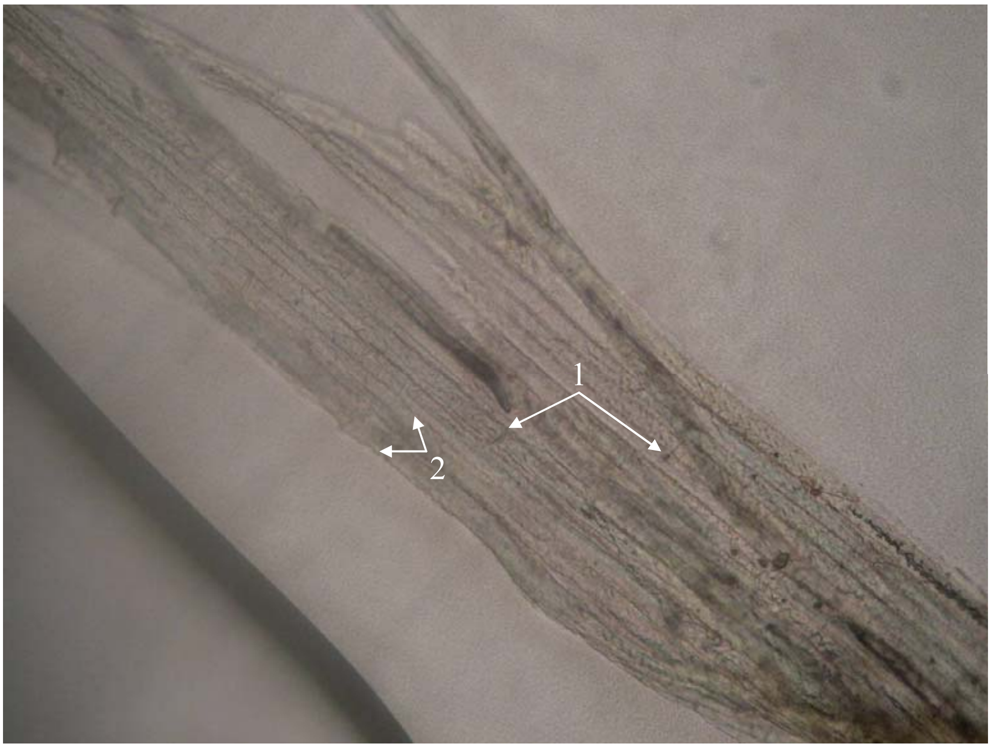


Photo X.53: Only a few cell walls recognisable (1), differs from *Poaceae* as cells have a milled edge (2).

III Dicotyledons

III.a Trees – sharp-edged cells

Betula pubescens

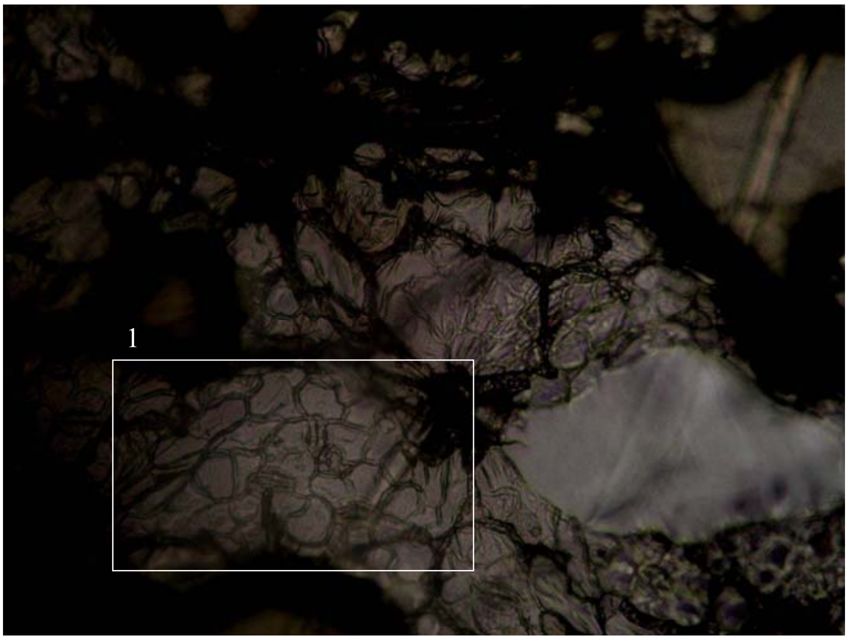


Photo X.54: Large stomata, 6 to 8 cells around stomata (1), cells fit like a puzzle but they are not extremely buckled.

Cells of *Salix* species are in web form with no rounded corners, they look roughly like a honeycomb or a web structure.

Salix repens

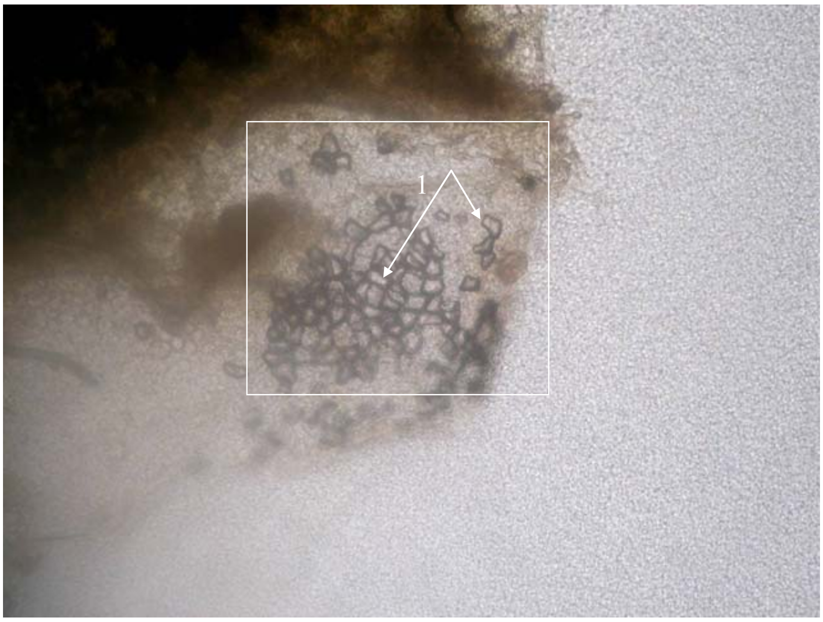


Photo X.55: Cell walls seem to be more straight and tough (1), than those of *Salix cinerea*. Cells are +/- 10µm long.

Salix cinerea

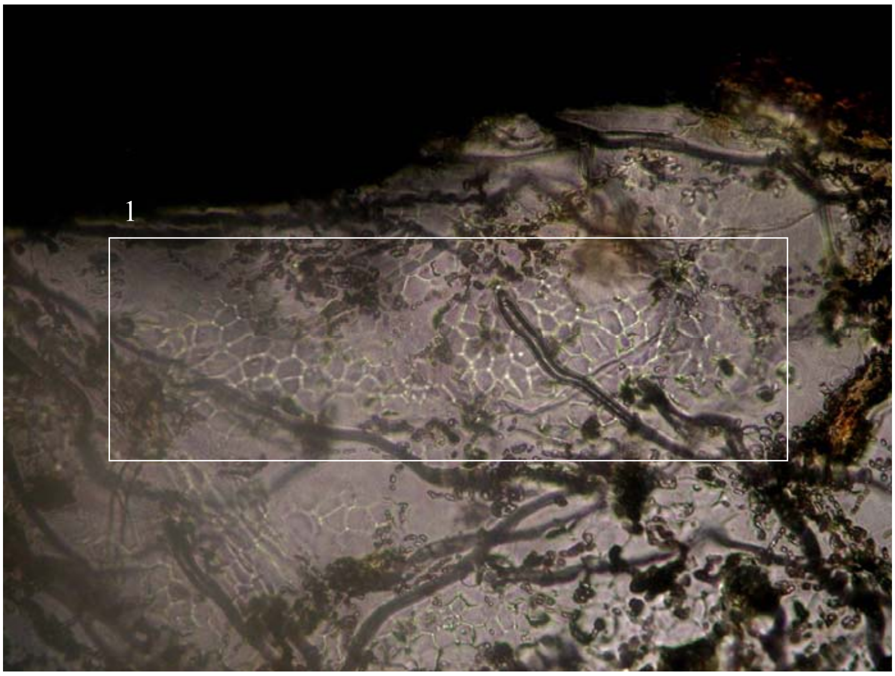


Photo X.56: Cell walls seem to bend towards inside (1), has few stomata, 8 cells around stomata. Cells are +/- 15µm long (around 12 cells can be counted in a radius of 20 x 10 zoom). Cells have a very similar size, in contrast to *Sorbus aucuparia.* Sometimes trichomes are visible.

Salix pentandra

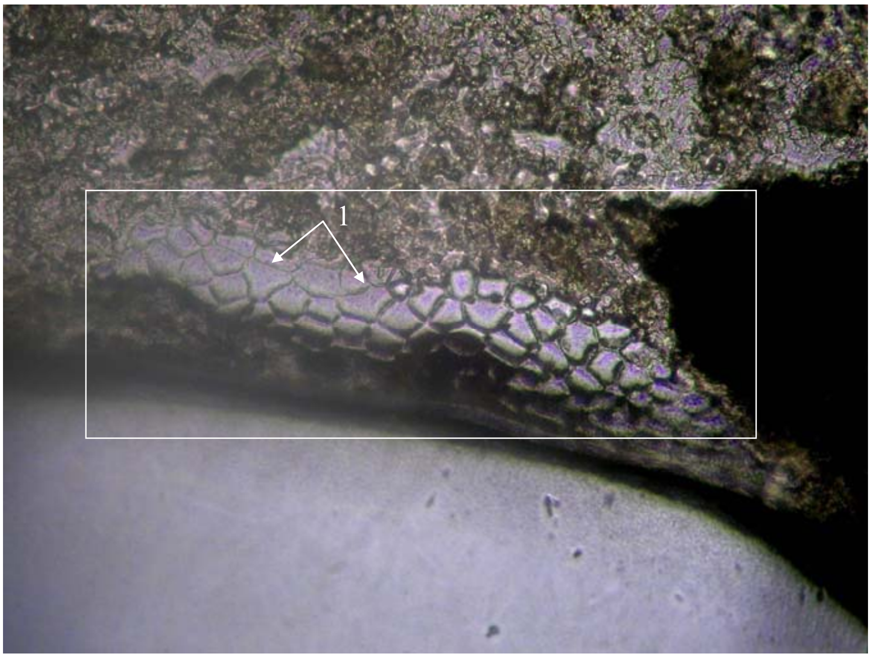


Photo X.57: Cells are much larger than those of *Salix cinerea*, > 15µm. Often triangular cell forms occur (1). *Salix pentandra* has few stomata with approximately 6 cells around.

Sorbus aucuparia

Photo X.58: Cells resemble those of *Salix cinerea* but have a more irregular size.

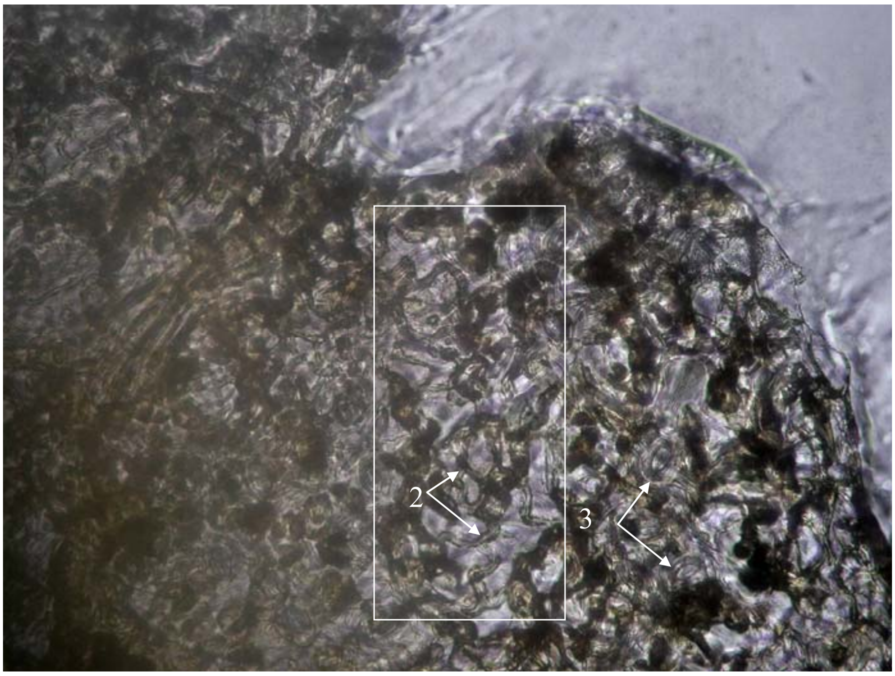


Photo X.59: Cell walls may also be buckled (2). Stomata are large (3).

Quercus robur

Photo X.60: Many cells are squared, with straight cell walls (1). *Quercus robur* has few stomata with 7 or 8 cells around.

III.b Trees - cells with rounded corners (puzzled form)

Alnus glutinosa

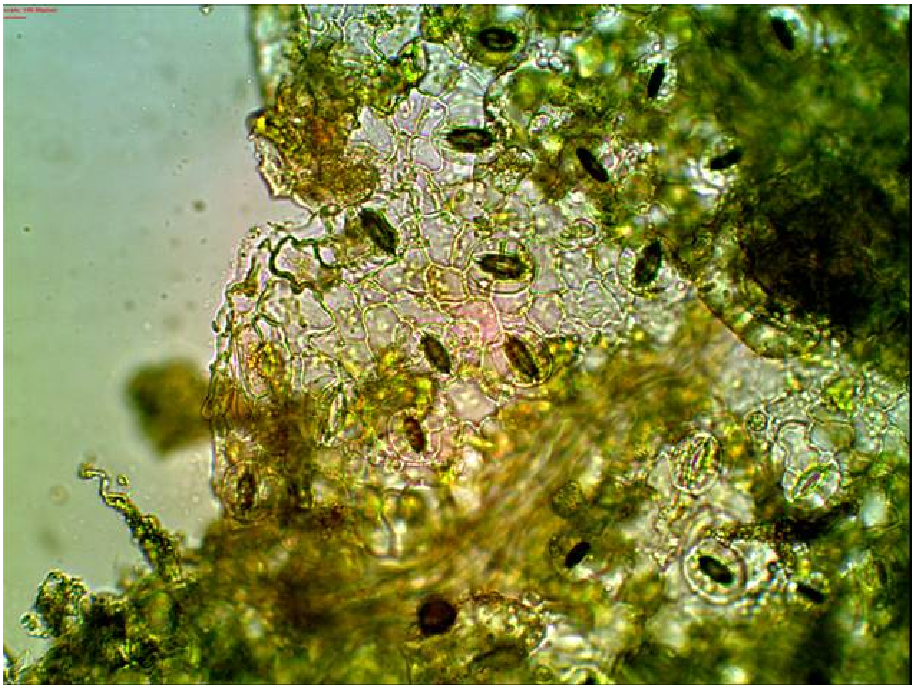


Photo X.61: Many stomata and puzzle cells, although not very buckled (photo: Hofman Emilia, 2010).

Corylus avellana

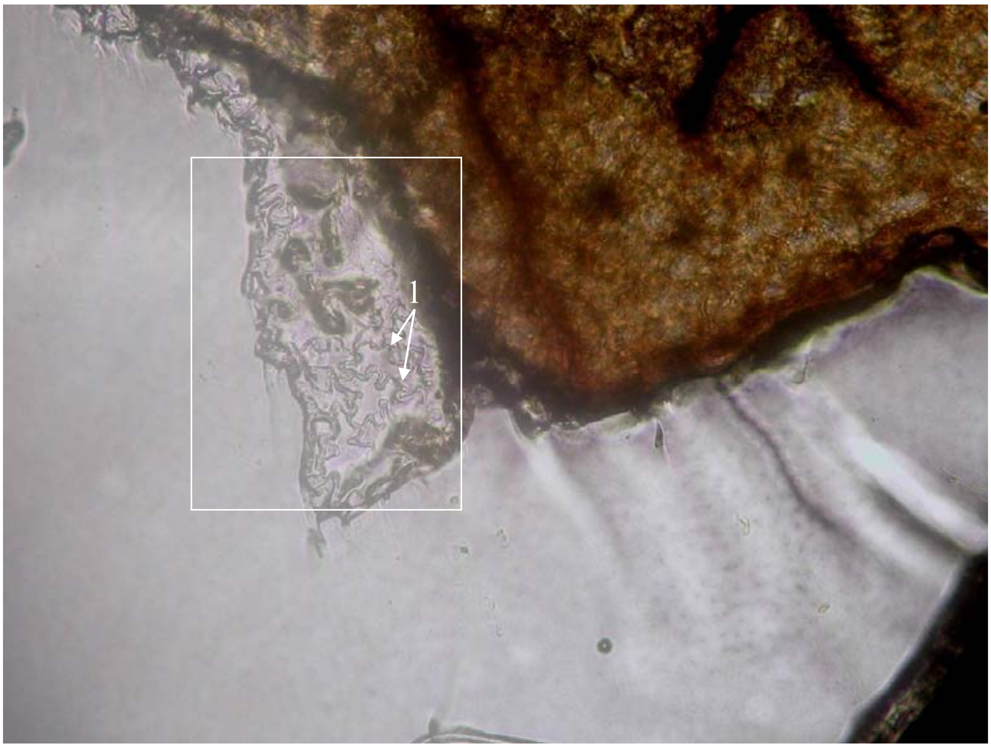


Photo X.62: *Corylus avellana* has very few stomata and has very small cells with a disorderly appearance. The puzzle cells have an irregular form (1).

Frangula alnus

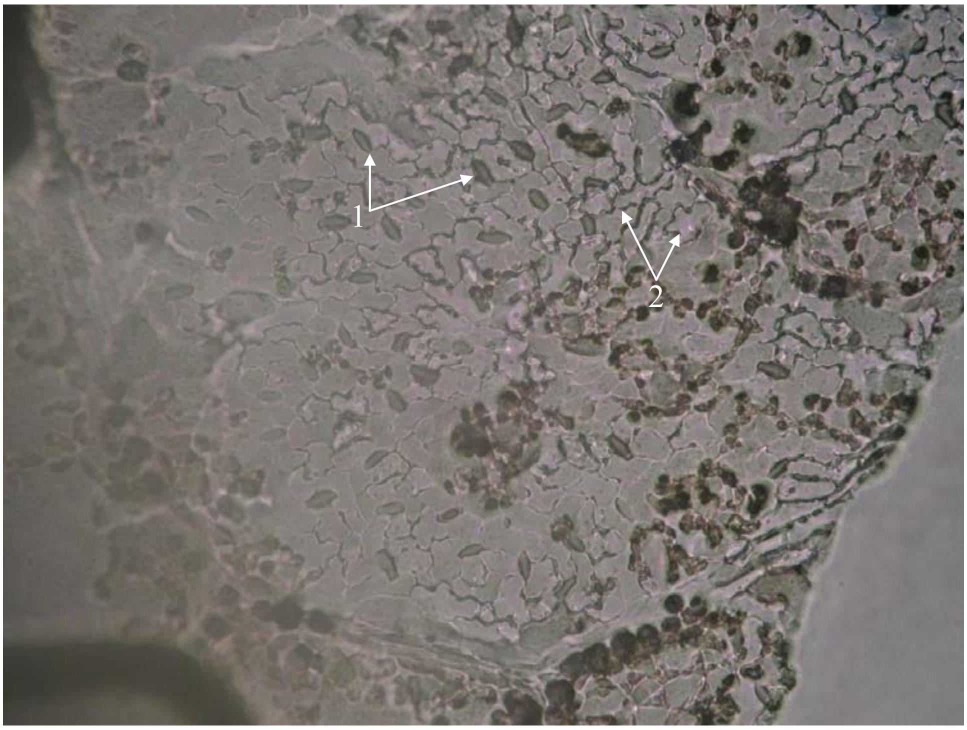


Photo X.63: *Frangula alnus* has a lot of stomata occurring in high densities (1) and small puzzle cells of irregular appearance (2) with 5 or 6 cells around the stomata.

Tilia platyphyllos

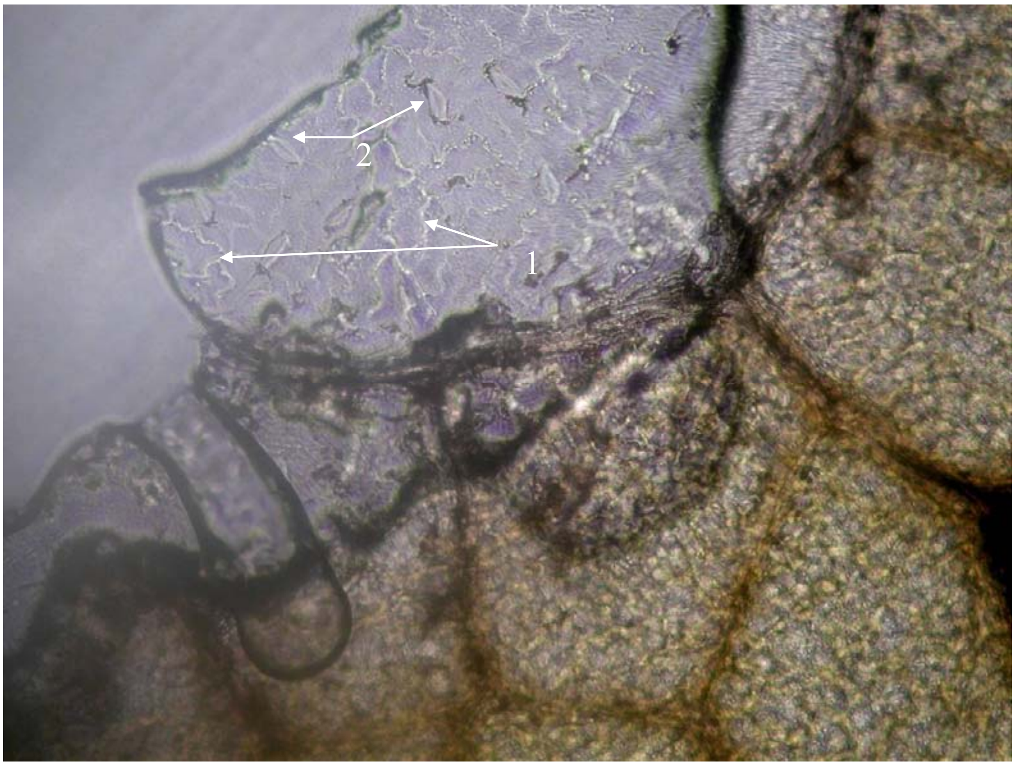


Photo X.64: *Tilia platyphyllos* has quite large puzzle cells (1) and has a lot of stomata, occurring in high densities (2) with approximately 8 cells around the stomata

Viburnum opulus

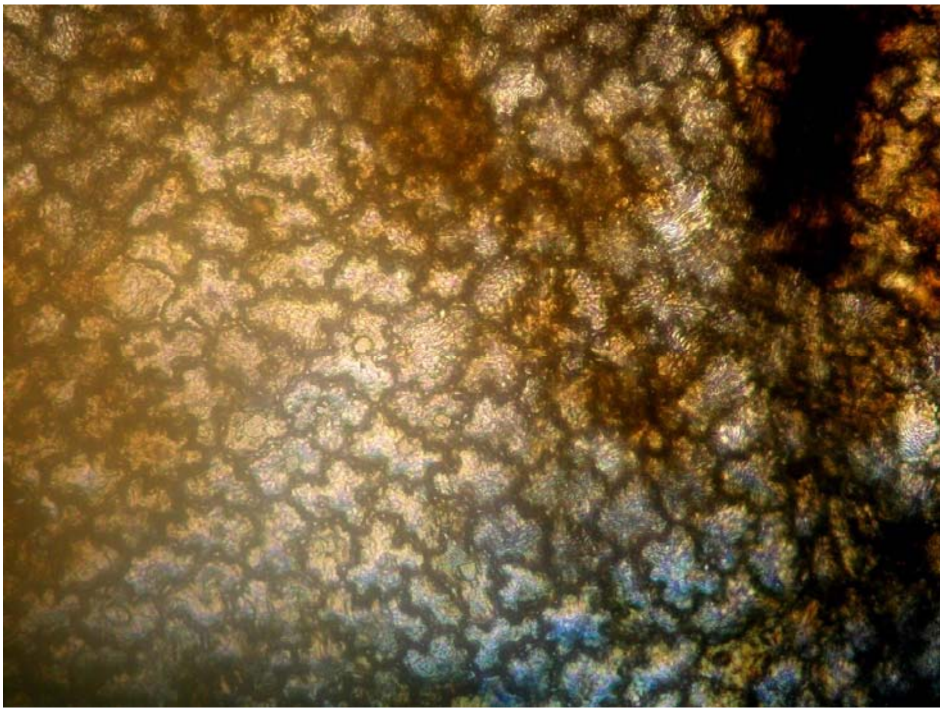


Photo X.65: Puzzle cells have a quite regular form, they look like simplified clouds, with only few stomata.

Twigs

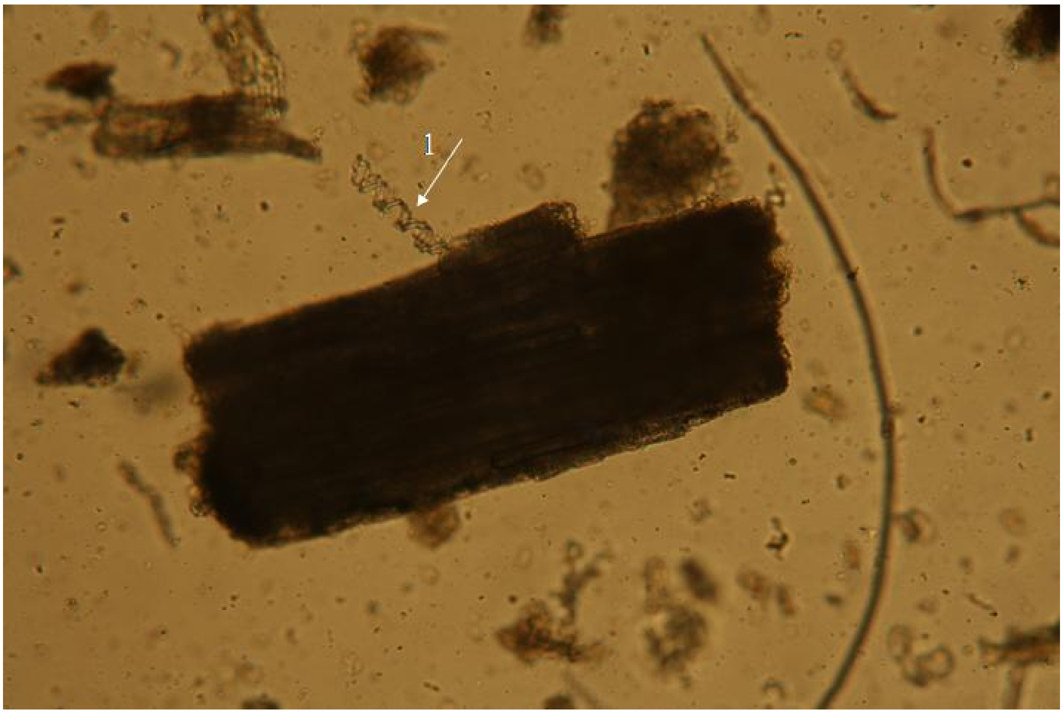


Photo X.66: Brown veins, of which the fibrous pattern is barely recognisable, are parts of tree species. Often curls are visible.

IV Herbs

Nuphar luteus

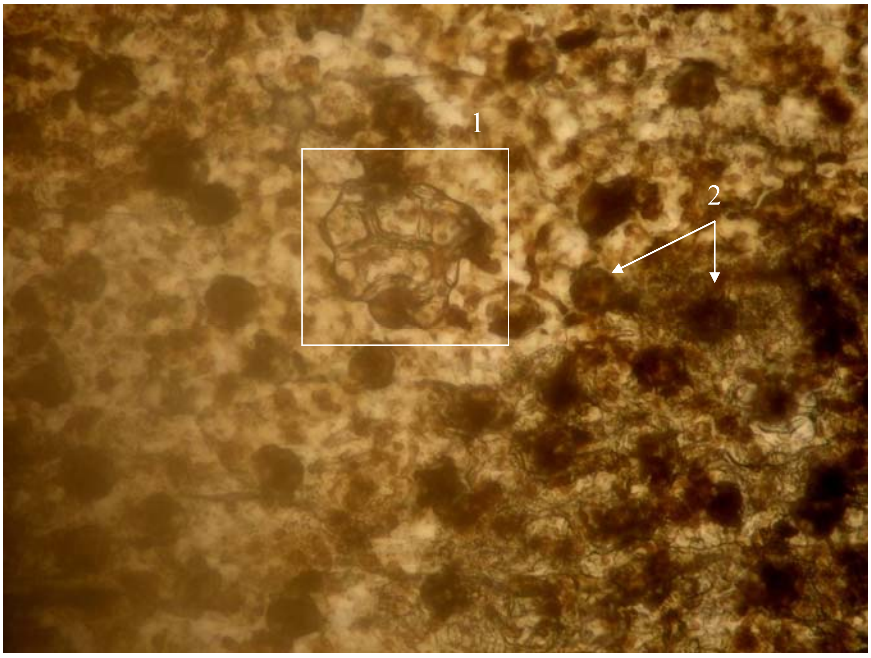


Photo X.67: *Nuphar luteus* has pentagonal cells (1) but the round dark balls (2) are the best characteristic to recognise this species (2).

Potentilla palustris

Photo X.68: *Potentilla palustris* has rather round cells organised in lines and is as a whole very structured.

Menyanthes trifoliata

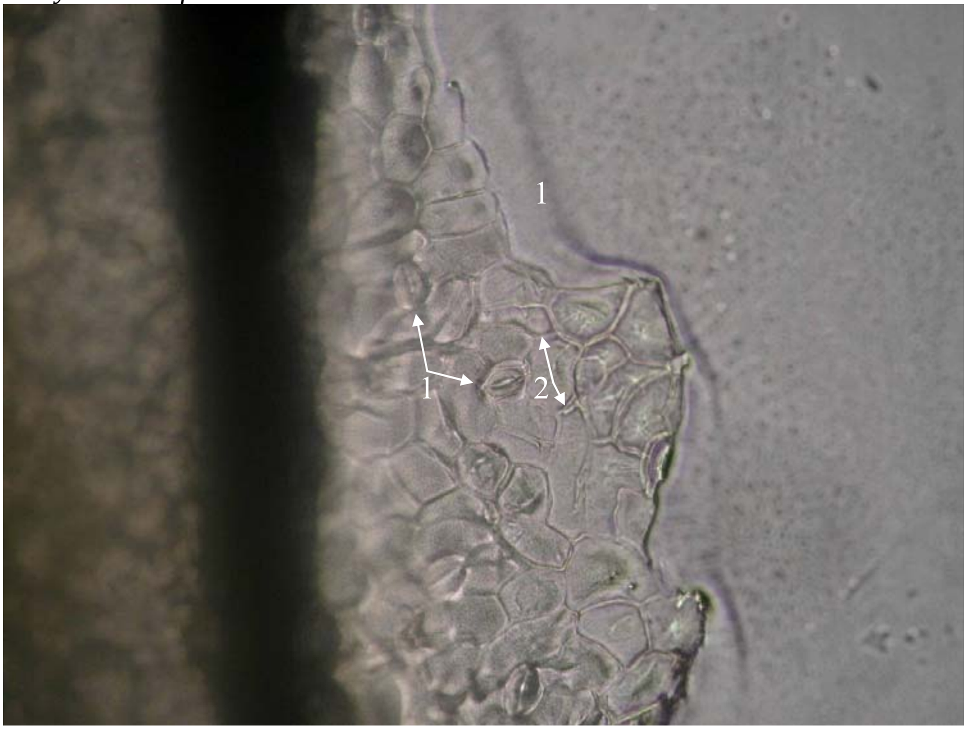


Photo X.69: *Menyanthes trifoliata* has well visible, large stomata, with 6 to 8 cells around. Cells are rather large but they differ in size (2).

Eupatorium cannabinum

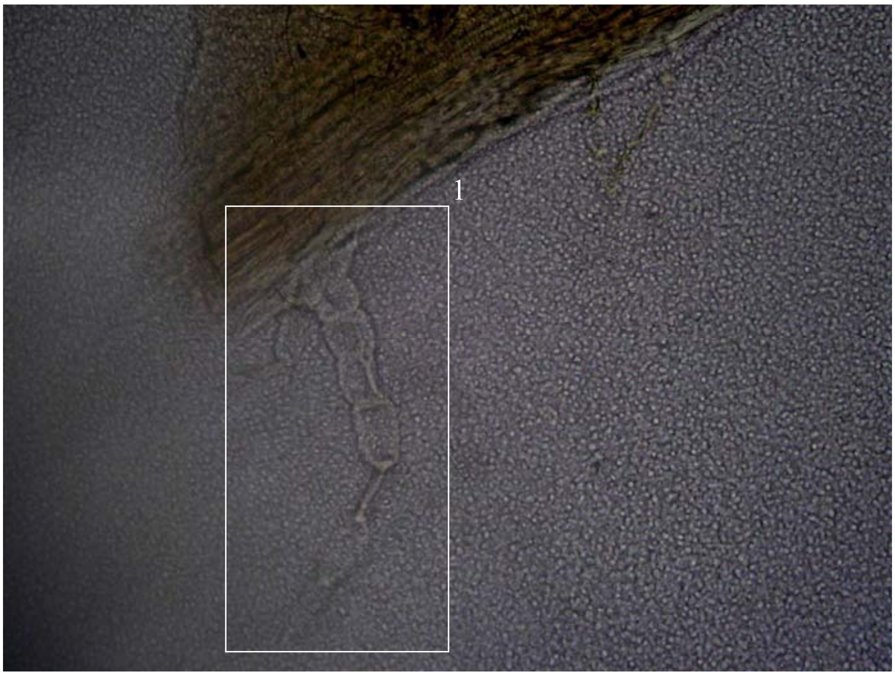


Photo X.70: *Eupatorium cannabinum* has rather small cells in rows in comparison with *Menyanthes trifoliata*. But most remarkable: its cells are rectangular with rounded corners.

Caltha palustris

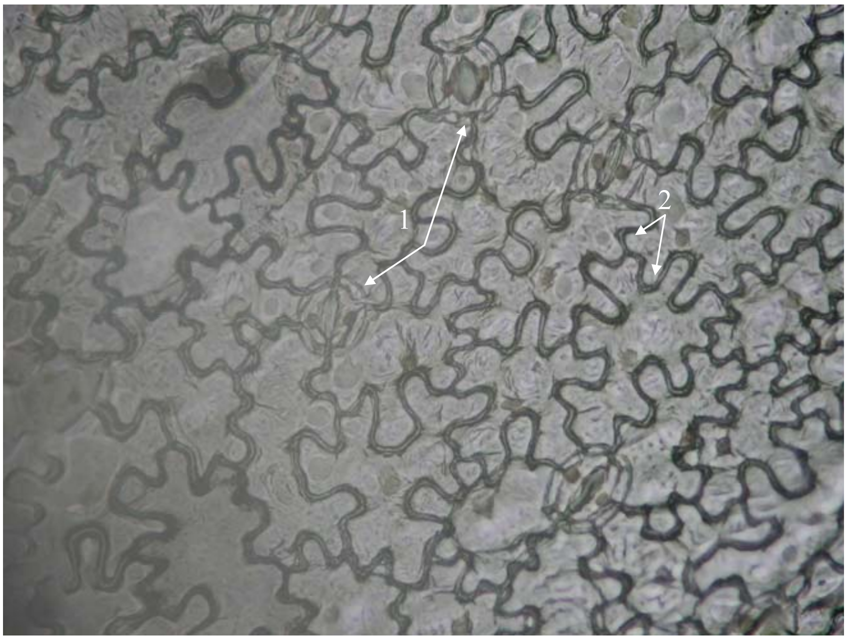


Photo X.71: Stomata (1) and cells (2) are very large and easily recognisable. Cells have a quite regular form. *Caltha palustris* has 5 to 7 cells around the stomata.

Vaccinium myrtillus

Photo X.72: Puzzle cells are quite regular (1), 4 to 5 cells around stomata (2). Stomata are small compared to those of *Caltha palustris* and occur also in some parts in high densities (3).

Hydrocharis morsus-ranae

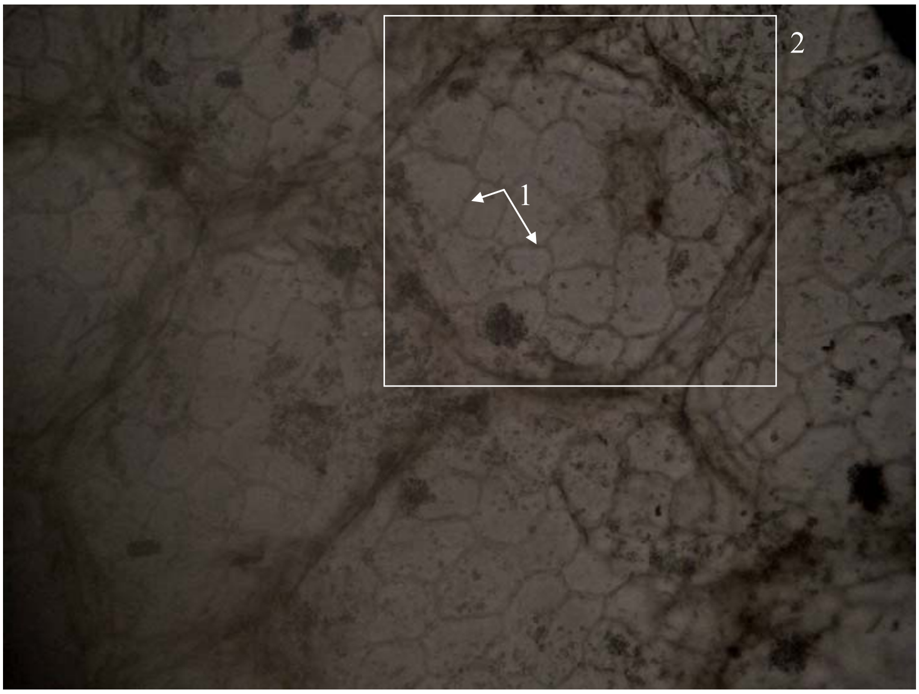


Photo X.73: *Hydrocharis morsus-ranae* has rather large cells (1), structured in bundles (2).

Ceratophyllaceae

Photo X.74: A part of the leaf is shown as the leaves are tiny.

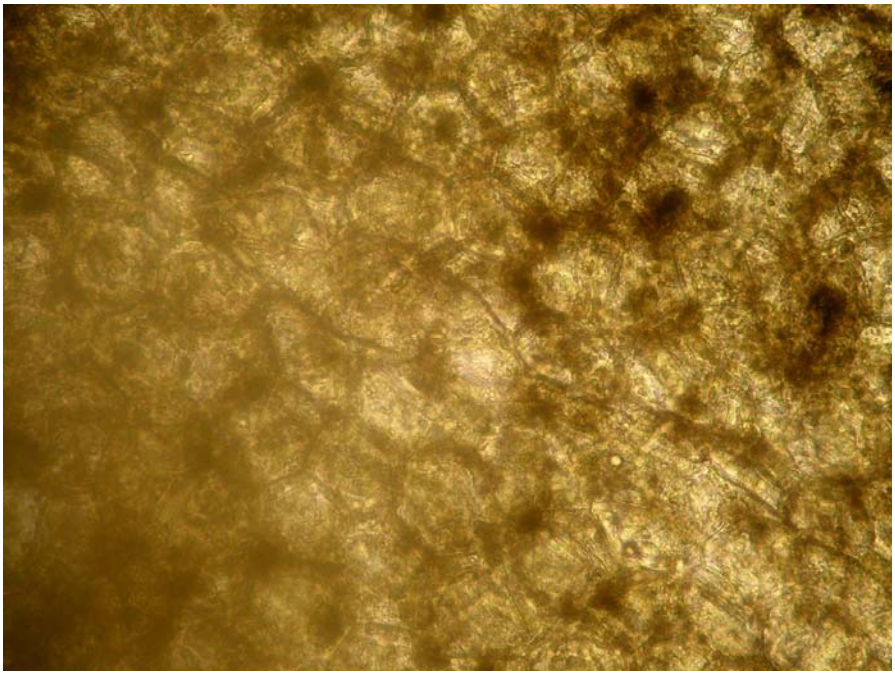


Photo X.75: A part of a seed is shown from a species of the family *Ceratophyllaceae*.

V Gymnosperm herbs

Equisetum arvense

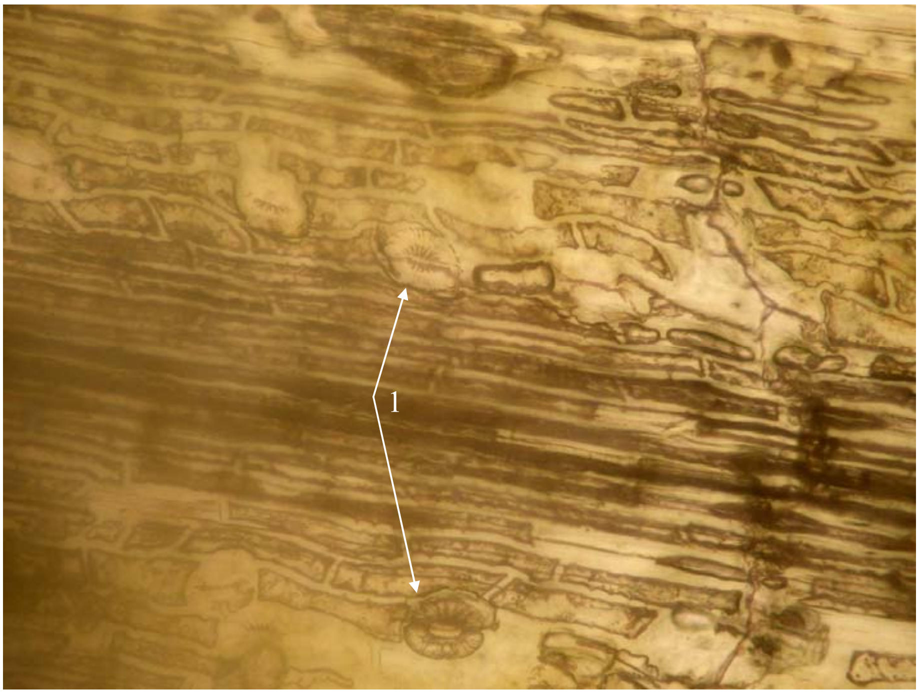


Photo X.76: Stomata have a very specific “wheel-like” appearance (1).

Thelypteris palustris (Moerasvaren)

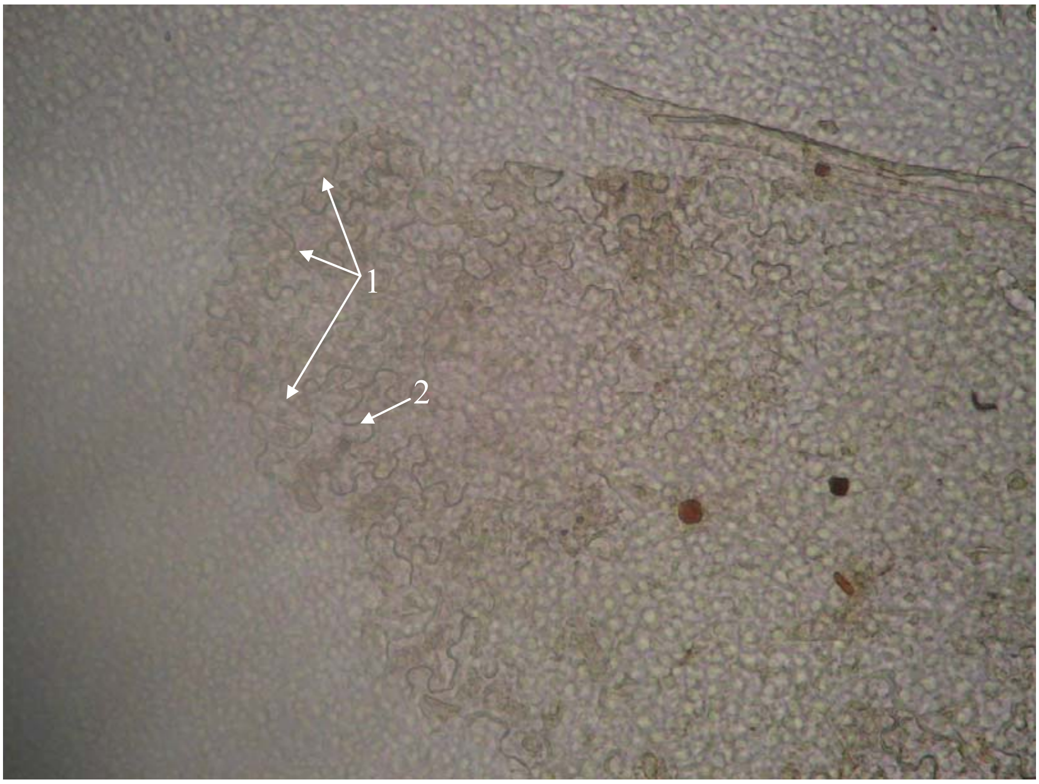


Photo X.77: *Thelypteris palustris* has large stomata (1) and large puzzle cells. But a cell is very difficult to distinguish from another cell next to it. It looks unstructured as a whole.

VI Mosses (Bryophyta)

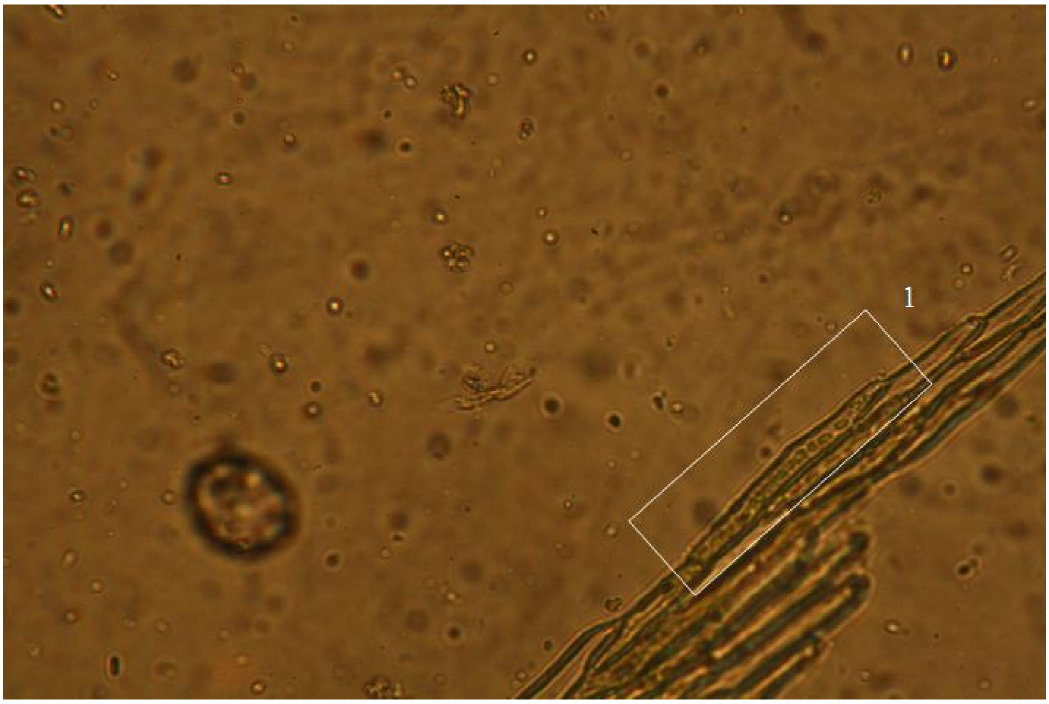


Photo X.78: Small spheres, being very remarkable to mosses (pers. inf. Kuijper D., 2010).

VEINS

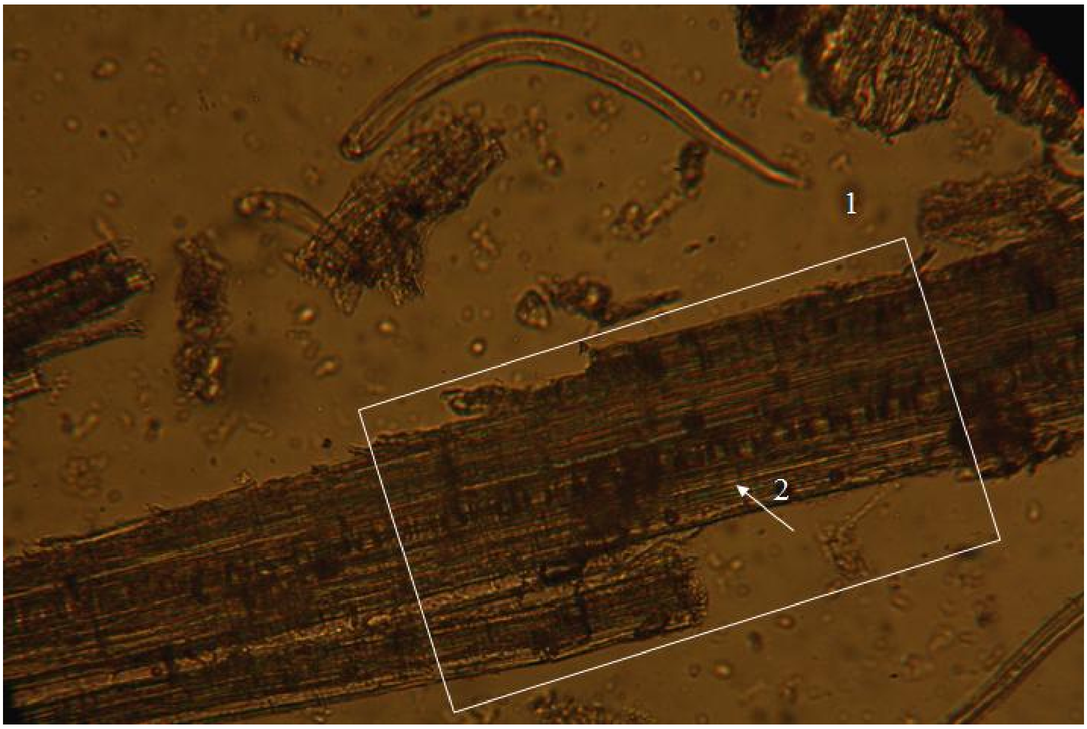


Photo X.79: A vein (1) being recognisable on the dense fibres that form a dense chequered pattern (2). These lighter variants than twigs (Photo 20) may be part of any of the plant categories. Often curls (fibres) are visible.

Photo X.80: Curled fibres (1) and raster structures (2) form typical characteristics of veins.