

# Prehistoric vegetation reconstruction of the archaeological site of Swifterbant

A pilot study based on macro-remains



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## ABSTRACT

Between 6300 and 6000 years before present Mesolithic people inhabited the sand dunes and creek levées in the Swifterbant area, The Netherlands. They had domesticated animals and probably started to grow cereal crops. The aim of this pilot study is to reconstruct the prehistoric vegetation in the area around the settlements by means of different analytical approaches released on a list of plant species occurring in the Swifterbant area. The list of species has been derived from macro-remains found in driftline material which was deposited on slopes of creeks. This species list has been used for several analyses in order to reconstruct the former vegetation of the Swifterbant area. An environmental characterisation, using average Ellenberg values of the archaeological species, indicated a division between a wet, brackish, nitrogen-poor habitat and a drier, sweet, nitrogenous habitat. Phytosociological analyses, based on the SynBioSys database using fidelity values, coexistence values and the results of the built-in Associa program, indicated the presence of several distinct vegetation types, the drier ones also differing in successional stage. After a discussion of the results of the analyses, the community types *Ruppion maritimae*, *Atriplicion littoralis*, *Arction*, *Echinochloa-Setarietum inops*, *Charetum canescentis* and *Chenopodio-Oxalidetum fontanae* resulted as good candidates for the former vegetation. A gradient analysis, performed with seed bank data of reference vegetation types, positioned the archaeological species generally between brackish grassland and dry heathland/forest edge vegetation. Furthermore, species response curves, showing the relationship between seed bank and standing vegetation, did not result in useful information for vegetation reconstruction here but may be helpful as a method in future research. Seed trait analysis showed that most archaeological species had either one or two large-distance dispersal adaptations. The final vegetational picture of the Swifterbant area is one including brackish wetland communities in the wet areas as well as mesic to dry, ruderal vegetation types on the higher, human-influenced elevations. The most important critique on this work is that the comparison between driftline material and seed bank or vegetation data to reconstruct the former vegetation is subject to errors because the way driftline material builds up is distinct from the way seed banks or standing vegetation builds up. Better would be to take archaeological seed bank samples and compare them with present day seed bank samples with their vegetation recordings.

Cover picture: Reconstruction of a 25 to 45 year old Neolithic Swifterbant man based on a skeleton with skull found in the Swifterbant area. Copyright M. d'Holloosy.

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## INTRODUCTION

### *VEGETATION RECONSTRUCTION*

The reconstruction of former vegetation can be approached by different methods. Besides the use of pollen and spore diagrams to follow the changes in vegetation through time, macro-remains, mostly seeds, are also commonly used for vegetation reconstruction. For both approaches, palaeoecologists use the basic assumption that (changes in) the densities of pollen or macro-remains reflect (changes in) the densities in standing vegetation. Another common assumption is that species found are species present.

These assumptions should be taken with great care. Soil seed bank ecologists primarily deal with the question how the seed bank can show strong deviations from the standing vegetation, both quantitatively and qualitatively. Seed production, seed predation, seed dispersal, seed dormancy and seed shape are examples of factors usually differing from one species to another. The soil seed bank composition is directly influenced by these kinds of factors. For example, species producing more seeds per individual are likely to have a higher input in the soil seed bank than species with a lower individual seed production. Or, species with a transient seed bank will have a smaller input in the soil seed bank than species with a long-term persistent seed bank. In the latter case, seed bank recordings may even be different according to the season in which sampling took place. And seeds may disperse to sites where the species does not occur.

In a palaeoecological context, it becomes even more difficult to translate the soil macro-remains to former standing vegetation. Factors as taphonomy (the study of decay of macro-remains) and phytosociological change due to evolution, subtle climate change, ecological processes like migration and invasion, or human influences like agriculture complicate the vegetation reconstruction (Cappers 1994). In this report, knowledge on recent plant communities is used to reconstruct former vegetation composition. However, plant community types are likely to have changed over time in their qualitative and quantitative composition due to above-mentioned processes. For example, it is known from studies on recent plant invasions that invasive species can alter community compositions (Alvarez & Cushman 2002). It is not unlikely that the collection of community types that is found today is different from prehistoric times and that neophytes changed plant community compositions.

In archaeobotanical research, which deals with vegetation remains in human-influenced sites, differences in plant community composition due to human-induced effects have also been found. For example, before the introduction of the mouldboard plough which turns the soil upside down, acres were ploughed by the scratch plough which consisted of a vertical wooden stick that was dragged through the topsoil. This enabled perennials to persist more easily in the fields. With the mouldboard plough, however, a shift in weed species composition occurred. In general, perennials made way for annual species (Cappers, pers. comm.).

The latter two paragraphs showed that the uniformitarian assumption, implying that present-day processes are identical to processes that took place in the past, cannot be straightforwardly made, due to both natural and human-induced effects on vegetation (Cappers 1994). In the context of archaeobotany, where research sites are by definition directly affected by man, uniformity may be even harder to assume. Human culture develops relatively fast compared to evolutionary and ecological processes and much of prehistoric human-induced processes remains unclear. In addition, much

archaeological knowledge is based on and restricted to hermeneutics, which makes quantitative assessments of the strength of human influences difficult. This is inherent to archaeological research, as it can only interpret a scarce number of findings of past civilisations; deductions based on densities of finds should be taken with great care in archaeology as it is often subject to biased sampling. However, the interpretation of archaeological finds may explain deviations in plant community composition from present-day circumstances, although care should be taken not to generalize too quickly.

It seems as if the mixture between soil seed bank ecology and archaeobotany is indeed at a crossing point of the Sciences and the Arts using both empirical methods and hermeneutics to be able to make sound conclusions. However, this report, describing an attempt to reconstruct the former vegetation of the archaeological site of Swifterbant, is biased towards empirical data analysis. And, as explained above, since it deals with archaeobotanical samples, it must be kept in mind that a substantial part of deviations from present vegetation composition may not be explained because of inadequate (quantitative) knowledge of prehistoric societies.

### ***INTRODUCTION TO SWIFTERBANT***

The Mesolithic Swifterbant people, named after the nearby present village of Swifterbant in the polder of Flevoland, The Netherlands, inhabited the area from approximately 6300 to 6000 years before present (BP; all data are calibrated) (Figure 1) (Raemaekers 2006). The main question addressed in this report is what kind of vegetation and landscape dominated in the Swifterbant area during the habitation by the people of the Swifterbant culture. In the remaining part of this introduction a short review will be given on the geography of the area around 6000 years BP, on human settlement in coastal areas and on the past archeological research at the Swifterbant site. Thereafter, the questions and the approach of the actual project will be introduced.

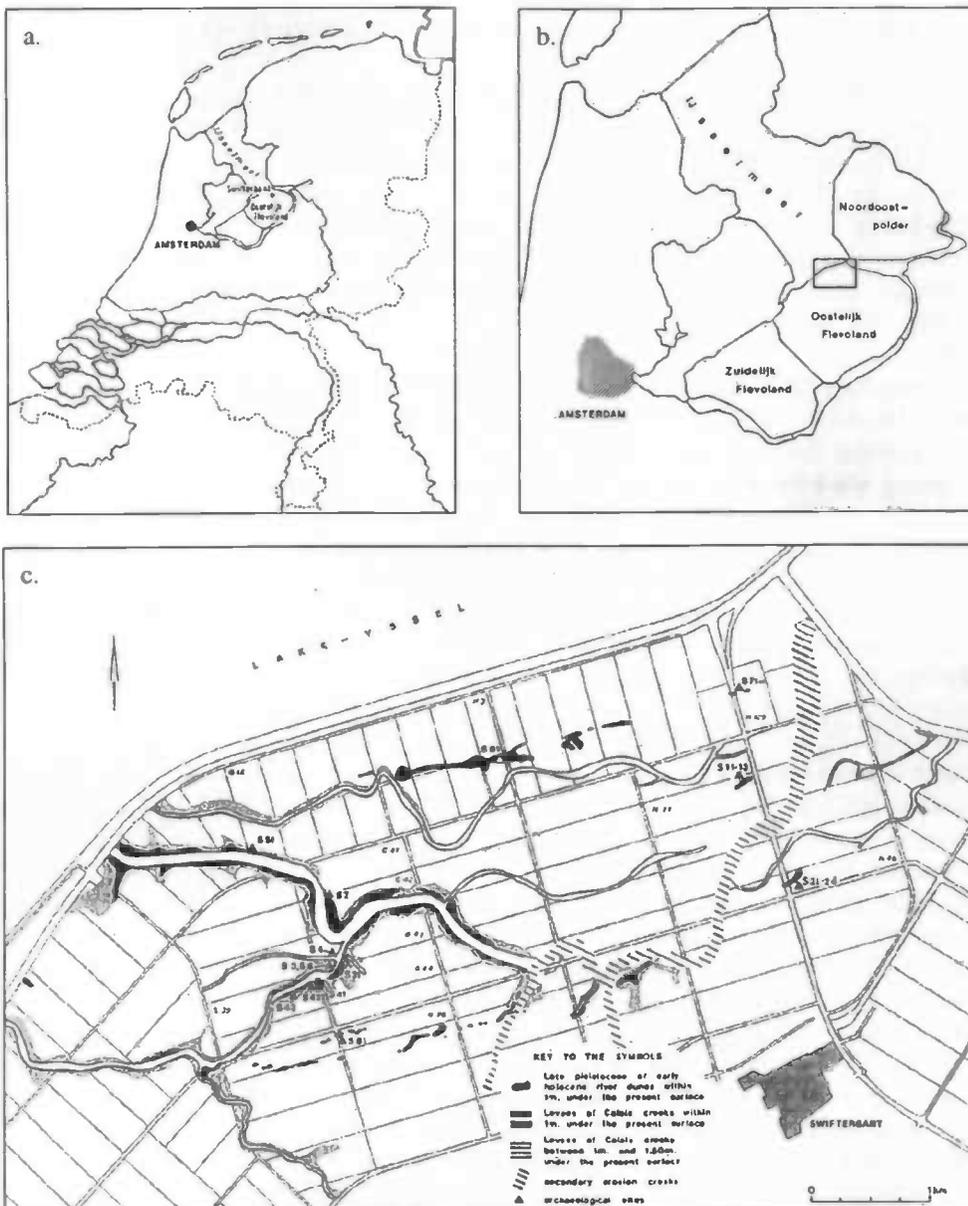


Figure 1. Maps showing (a) The Netherlands with the village of Swifterbant in Oostelijk Flevoland, (b) an enlargement of the Flevoland polders within which the rectangle indicates the enlarged area in c. The creeks, levées and dunes from around 5300 years BP are plotted on top of the actual topography. The map also shows the archaeological sites with their site numbers. Figures a. and b. adopted from Van Zeist & Palfenier-Vegter (1981), figure c. from Deckers *et al.* (1980).

## PALAEOGRAPHY AND PALAEOECOLOGY OF THE NETHERLANDS

Around 8000 BP the sea level lies 20 m below the present level and is rising fast since the ice of the last glacial period started to melt (Figure 2). Due to this strong sea level rise the Holland tidal basin was created between 8000 and 6000 years BP. This basin lay in the former delta of the Overijsselse Vecht River and the Eem River in the lake IJssel area and in the area which is now the province of Noord-Holland. Until 7000 years BP this increase went so fast that formation of peatland or even sedimentation could not keep pace. The old peatlands drowned and gullies formed (De Mulder *et al.* 2003).

Because the tidal basin had a lagoon-like structure, the incoming water from the IJssel and Eem rivers probably made the water sweet. Sea water mixed only with the river water where the river water flowed out of the basin into the sea. But over time the ongoing sea-level rise and the strong influence of the sea on the shore created a brackish environment in the basin with many tidal gullies due to wider openings between sea and basin. The oldest gullies in Noord-Holland date from before 6300 years BP. Clay could only precipitate in the inland areas of the creeks where the current is less strong. The two maps in Figure 3 show the sea level rise, the increase in size of the Holland tidal basin and the formation of inland gullies (De Mulder *et al.* 2003).

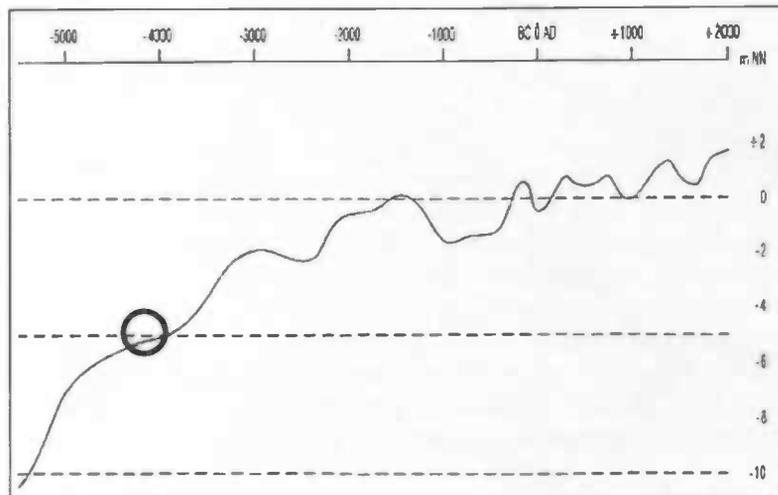
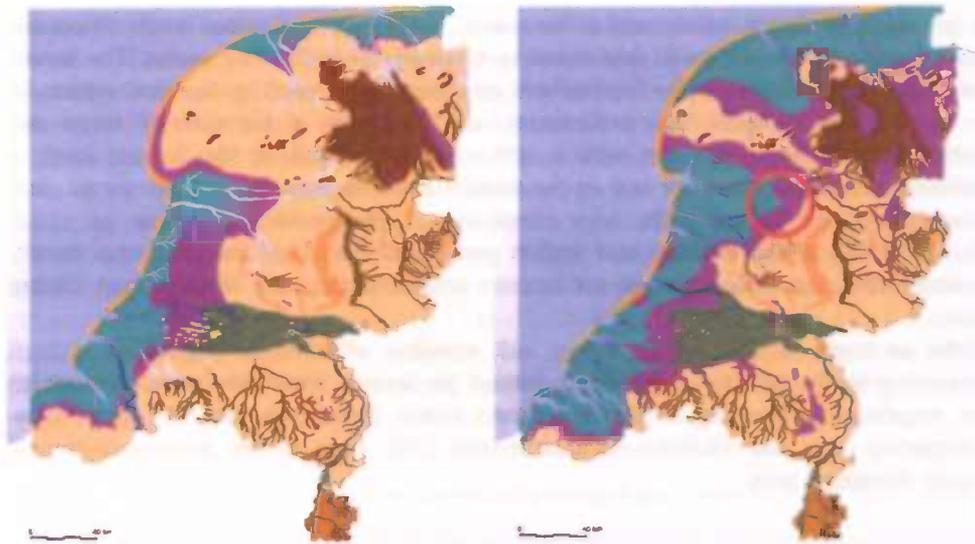


Figure 2. Sea level changes from 7500 to 0 years BP. The encircled part indicates the time-frame of the Mesolithic Swifterbant culture. Adopted from Behre (2004).



**Figure 3.** Palaeogeography of the area which is now The Netherlands at 6500 BP (left) and 5100 BP (right). Yellow, dunes; green, tidal area; purple, peat bog; beige, Pleistocene sand deposition. The red circle indicates the Swifterbant area. Adopted from De Mulder *et al.* (2003).

Over time the sea-level rise became slow enough for clayey material to be precipitated in the basin and somewhat later the formation of peat started at the edges of the basin. Sedimentation and formation of peatland could finally keep pace with the sea-level rise (De Mulder *et al.* 2003). Between 6150 and 5900 years BP the sea-level rise came almost to a halt, whereafter sea-level rise accelerated again (Figure 2). The general understanding is that no regression took place within this period of slow sea-level increase. A regression is the increase in land area at the expense of the sea, either by aquatic or marine vegetation succession or by decreasing sea-level or by both. A transgression, the opposite of a regression, is the decrease in land area by erosion or sea-level rise or both. However, this period of slow sea-level rise between 6150 and 5900 demarcates the Calais II and Calais III transgressions, and, locally, the slow sea-level rise may have resulted in salt-marsh growth and peat formation, especially in inland areas (Behre 2003). Therefore, in inland places like in the Swifterbant area where possibly peat and salt marshes started to form, one can speak of a (semi-)regression. Towards the end of this semi-regression, people gave up habitation of the Swifterbant area but possibly continued agricultural practices there during summer. In short, the Swifterbant culture existed at the time of decreasing growth of the Holland tidal basin and ended when inland salt marshes and peat bogs started to expand.

The Swifterbant site was probably located close to the edge of the Holland tidal basin and consisted of gullies and creeks with levées at the sides. In addition, former river dunes are present, a remnant of the IJssel and Overijsselse Vecht river delta (De Roever 2004). The transition from sweet to brackish water must have been decisive upon the vegetational characteristics of the area. In the beginning, riverine vegetation was probably present, while slowly more salt-tolerant species must have invaded the area. Other dominant communities probably belonged to the classes *Phragmitetea* (08; official community type numbers used in SynBioSys, Hennekens *et al.* 2001), *Franguletea* (36) and *Alnetea glutinosae* (39), or reed-, willow- and alder-based communities, respectively.

At the edges of rivers, creeks and at the coasts, recurring high water levels ultimately create levées due to sediment deposition in relatively slow-flowing water. The levées and former river dunes in the Swifterbant area have been used by the first settlers in the coastal area to build their settlements on. The levées at the sides of rivers and creeks used to be overgrown with a softwood willow-belt at the lowest level, a hardwood *Fraxinus excelsior* belt in the middle and with hardwood *Quercus sp.* and *Ulmus sp.* at the highest parts. *Acer campestre*, *A. platanoides* and *Alnus sp.* could also be found at the middle and higher part. This Fraxino-Ulmetum was mostly cleared before the Roman period and became extinct in the early Middle Ages (Behre 2004).

While in front of the levées, either salt marshes or riverine vegetation existed depending on the salinity of the water, behind the levées, low-lying sweet to brackish bog vegetation existed up to the pleistocene sands. Parvocaricetea (09), Oxycocco-Sphagnetetea (11) and Molinio-Arrhenatheretea (16) may be the phytosociological classes dominant here.

### **HUMAN SETTLEMENT IN COASTAL ENVIRONMENTS**

Due to the dominant sea currents, the barrier islands came into existence about 8 millennia ago, creating a shallow bay at its rear. The mud flats and sandbanks created habitat for a wide diversity of sea life which, in turn, could have been attractive to Mesolithic hunter-gatherer-fishermen of which is known that they lived at that time in the higher areas of The Netherlands. Evidence for this presumed earliest human presence in the coastal areas, however, is scarce as the high dynamics of the area scattered, destroyed and buried any remains. After the formation of the Wadden Sea area, salt marshes as well as mires and bogs started to expand in that area. The salt marshes were formed in salt to brackish, shallow waters whereas the mires and bogs were formed in the sweet-water influenced lowland areas between the higher pleistocene depositions and the coastal levées created by the tides. They expanded rapidly in times of regression and were partly washed away or drowned during periods of transgression, as explained in the section above. Peat formation in both sweet and salt habitats occurred predominantly during periods of regression. The most extensive salt marshes, mires and bogs were present in the outer edges of the Wadden Sea area (present Denmark and the province of Holland with the Lake IJssel), since these locations were subject to relatively low tidal impact compared of the middle part of the Wadden Sea (Behre 2003; 2004; Knottnerus 2005).

The oldest direct evidence for human settlement in the Wadden Sea area dates back to the transition from the Mesolithicum to the Neolithicum during the Atlanticum (Table 1). Hunter-gatherer-fishers started to keep cattle and probably grow crops on the fertile slopes of creeks and rivers. In addition, fishing and fowling was improved (Louwe Kooijmans 1993). Knowledge of coastal inhabitants on agricultural practices may have come from the Bandceramic Culture which started farming in a nomadic lifestyle with temporal settlements in the Limburg Löss area around 6300 BP. In the lower parts, like in river and coastal areas, people built temporary accommodations on Late-Glacial river dunes which stand above the peatland and the river area (Louwe Kooijmans 1985). The peatlands just behind the coastal zone remained uninhabited at that time (De Mulder *et al.* 2003).

The Swifterbant and Ellerbek-Ertebølle cultures have been identified in the Zuiderzee (present Lake IJssel and Flevoland) and on the banks of the Elbe River near present Hamburg, respectively. Both are seen as related to the later Vlaardingen Culture (5500-4700 yrs BP) and Single Grave Culture (4900-4300 yrs BP). All named cultures are strongly related to the Funnel Beaker Culture. They probably started to exploit the coastal areas by means of summer camps. At a later stage they permanently settled these regions (Louwe Kooijmans 1993).

Apart from the agricultural practices on the fertile slopes and the grazing of livestock, the Swifterbant and Ellerbek-Ertebølle cultures did not modify their environment substantially. Only in the Bronze Age (Table 1) did farmers start to cut down thickets and woodland for timber, fuel and fodder. In addition, ditches were built around their fields and sometimes whole farmyards were raised against the effects of increasing groundwater levels (Behre 1995a and 1995b in Knottnerus 2005).

**Table 1.** Timetable of geological and archaeological periods as appropriate for North-West Europe. (De Mulder *et al.* 2003)

Geological periods		Archaeological periods	
Holocene	11500 – 0 yrs BP	Mesolithic	11500 – 6500 yrs BP
Mid-Holocene	8300 – 2600 yrs BP	Neolithic	6500 – 4100 yrs BP
Atlanticum	8300 – 5000 yrs BP	Bronze Age	4100 – 2600 yrs BP
Subboreal	5000 – 2600 yrs BP		

## **SWIFTERBANT CULTURE**

### ***Former research***

Between 1950 and 1957 the polder of Oostelijk Flevoland has been created in the Lake IJssel. This lake was formerly called the Zuiderzee which stood in open connection to the Wadden Sea area before the construction of the Afsluitdijk in 1932. The accidental finding of pottery and firestone in a ditch on the former sea bottom was the first sign of human use of the area and triggered thorough geological and archaeological investigations. The impoldering gave the opportunity to easily investigate the landscape as it used to be at times of lower sea-levels. In the north-western part of Oostelijk Flevoland, a tidal-creek and river-dune system was discovered at 5-6 m below the present sea-level (Figure 1c; De Roever 2004).

From 1962 to 1967, G.D. van der Heide from the Rijksdienst voor de IJsselmeerpolders investigated the Swifterbant archaeological site. He observed that prehistoric people were living on a series of river dunes and along the shores of the Mesolithic to Neolithic precursor of the present IJssel River. Subsequent research from 1972 to 1979 conducted by Prof. Dr. J.D. van der Waals from the Groningen Institute of Archaeology (GIA) showed that the inhabitants were hunter-gatherers and later on hunter-gatherer-farmers which used the river dunes periodically. Because farming may have taken place, the Swifterbant culture represents a transitional culture from hunter-gatherer-based communities to farmer-based communities, thus from Mesolithic to Neolithic communities. It has been shown that crops of which macro-remains have been found in the Swifterbant area, can be grown on the upper salt marsh in The Netherlands (Van Zeist *et al.* 1976). Excavations resulted in evidence indicating that the residents hunted wild animals, gathered nuts and wild fruits, fished, kept cattle and possessed, and possibly grew, cereals. It was shown that from 6300

years BP a number of creeks were present in the area and that until 6000 years BP people were living on different locations on the shores of these creeks. Therefore, the maximum possible time of habitation on the levées was from 6300 to 6000 years BP (Raemaekers 2006). However, Deckers *et al.* (1980) showed that people intermittently made use of the dune area between 7800 – 5300 years BP, as has been estimated by means of radiocarbon dating on archaeological finds. Before the permanent settlement in the area, hunter-gatherers were already active there for a long time. The abandonment of the site is connected to the rising sea and groundwater levels. Other reasons may also have played a role. Salinisation of the water, for instance, may have threatened drinking water stocks and hampered agriculture. In addition, the sedimentation in the gullies may have complicated fishing practices on which the inhabitants may have relied partly.

Shoreline site S3, which was dug up in the 70s, showed the presence of cereal grains and chaff remnants of emmer wheat (*Triticum dicoccum*), bread wheat (*Triticum cf. aestivum*) and naked barley (*Hordeum vulgare nudum*) (Van Zeist & Palfenier-Vegter 1981). Chaff could indicate local growing of cereals because, the argument runs, the transport of cereal grains is assumed to occur after threshing of the spikes to reduce transport load. If so, growing of cereals must have taken place on small-sized acres because of the heterogeneous and small-scale landscape conditions (Casparie *et al.* 1977; Raemaekers 2006). However, Cappers (1998) states that grains left in spikes have higher resistance against fungal attacks and indicates that this practice occurred in Roman times and on the Dutch Veluwe. The finding of Cerealia pollen in appropriate soil layers argues in favour of agriculture, but this is only weak support as the determination of Cerealia pollen is difficult (De Roever 2004), so no final conclusion has been drawn yet. Louwe Kooijmans characterises the Mesolithic society of hunter-gatherers as a broad-spectrum economy in the light of risk spreading (hunting, gathering, fishing and farming, but also the growing of two types of cereals with different growth optima). The landscape diversity in the Swifterbant area is high with ditches, shores, marshland, river dunes. Marshland could be used for cattle grazing and the shores for wheat production. Having acres on shores has advantages as well as disadvantages: bad drainage and a higher risk of floodings, but also nutrient input by the sediment deposition during floodings. Archaeological research showed that the shores have been dugged which may indicate ploughing. This digging continued after the local people no longer lived in the area and the creeks were full with sediment (Raemaekers 2006).

A vegetation reconstruction for site S3 is performed by Van Zeist and Palfenier-Vegter (1981). They state that the inhabited levées contained trees of species *Quercus sp.*, *Ulmus sp.*, *Fraxinus excelsior*, *Malus sylvestris*, *Tilia sp.*, *Populus nigra*, *Betula sp.* and *Alnus sp.*. The river dunes are thought to have had a slightly different composition. The biggest diameter of tree remains found at the site was 11 cm, but most tree-trunk remains had a diameter of 4-7 cm (Casparie *et al.* 1977). The reason for these small sizes could be that the environment was too wet for thorough tree growth. However, remains of certain moss species and the high vegetational diversity indicate the presence of old trees. The wet soil was covered with reed and willow shoots by the inhabitants, which explains the high seed contents of these species in the settlement area. Many ruderal species were probably also present in the settlement, like Polygonaceae, *Urtica dioica*, *Atriplex sp.*, Chenopodiaceae, *Stellaria sp.* and *Plantago sp.* (Van Zeist & Palfenier-Vegter 1981).

On the lower, drier parts of the levées, an *Alnetea glutinosae* (elm-willow brook forest) and a riverine plant community with *Phragmites australis* and many Cyperaceae like

*Carex spp.*, *Schoenoplectus spp.* and *Typha spp.*, was probably present. In open water, *Potamogeton spp.*, *Menyanthes trifoliata*, *Alisma spp.*, *Caltha palustris*, *Nymphaea alba* occurred. Few marsh plants have been found. Some brackish species that have been found are thought to be derived from creeks which were periodically influenced by sea water (Van Zeist & Palfenier-Vegter 1981).

Charred remains of hazelnuts, an apple and cereals tell something about the vegetable diet of the inhabitants, and the dominant *Conium maculatum* could have been grown for its medicinal properties. Many other naturally occurring species have probably been used by the inhabitants but this could not be deduced from the abundances or condition of the remains (Casparie *et al.* 1977; Van Zeist & Palfenier-Vegter 1981).

### **Current research**

In 2004, GIA continued the research at the Swifterbant archaeological site S2 in cooperation with the Province of Flevoland and the State Service for Archaeological Heritage Management. They estimated the area of potentially interesting shores at 8.000 m<sup>2</sup> of which 16% has been dugged up by now. The area of potentially interesting river dunes was estimated at 120.000 m<sup>2</sup> of which 1% has been dugged up by now (GIA 2004; Raemaekers 2006).

Zoological research in 2005 by the GIA on site S4 showed the remains of dog (*Canis familiaris*), pig (*Sus domesticus*), cattle (*Bos taurus*), sheep and/or goat (*Ovis aries/Capra hircus*), beaver (*Castor fiber*), otter (*Lutra lutra*), wild boar (*Sus scrofa*), red fox (*Vulpes vulpes*) and red deer (*Cervus elaphus*). Pig and beaver occurred most often. Remains of water-related birds, mostly ducks, and sweet water fish as well as a sweet water snail have also been found (GIA 2005; De Roever 2004). Zeiler (1991; 1997) has reported on bone remains from site S3 and found some additional wild species.

The leading questions of GIA in the current research is whether the inhabitants of the shorelines have grown their own cereals locally or brought them in from somewhere else and consumed them on the spot. The actual trial to reconstruct the prehistoric vegetation may give insights into this question as agricultural activities often have profound effects on the local natural vegetation.

## PREHISTORIC VEGETATION RECONSTRUCTION

In this study, three samples of driftline material found at or close to site S4 have been investigated. This resulted in a list of species or higher taxa of which plant macro-remains, mostly seeds, were present in the driftline material. This dataset is central to this study in which analyses based on different methodologies have been performed in order to try to reconstruct the prehistoric vegetation of the Swifterbant area. A background question of this pilot study is whether different methodologies would give similar or different results. If different methodologies arrive at the same conclusion, it would strengthen the predictions that certain plant community type(s) was/were present. Henceforth the term seed indicates all plant macro-remains, and often the term 'species' is used when dealing with species listed in the archaeological dataset.

### Site description

Site S4 lies on the western edge of the big creek and borders a small gully on its southern side which separates it from site S3. Two samples of driftline material (named S22 and S23) have been taken from the excavation pit at site S4 (2006) and one (S21) from the excavation pit on the opposite side of the creek (2006) (Figure 4).

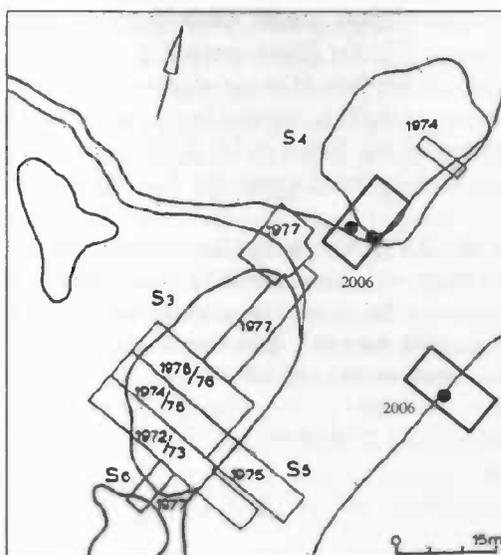


Figure 4. Map showing the origin of the three samples indicated by black dots in the 2006 excavation pits. Adopted from Deckers *et al.* (1980).

### *Seed collection*

After collection, driftline material was filtered through three filters of different mesh size in the order 2, 1 and 0.5 mm. Two liters of material have been investigated of each sample. Of sample S21, two extra liters have been checked for additional species, which resulted in *Sonchus asper* and *Sonchus arvensis* as additions to the species list. Macro-remains include seeds, fruits and other fragments and these have been identified at the lowest possible level. The raw archaeological data are given in Appendix A.

### *Methodologies*

Before introducing the methodologies, it should be emphasized that interpretation of the macro-remains found is not straightforward; especially the analyses based on relative abundances of the macro-remains should be interpreted with caution. For example, as mentioned in the first part of the introduction, not every plant produces the same number of seeds and not all seeds have been conserved for 6300 years. Also, plant species disperse their seeds to different extents, biasing random dispersal. Some species of which seeds have been found may not have grown there at all. Some seeds, due to their elongate shape, do not get incorporated into the soil layer but stay on top of it and will therefore not be conserved. Some species reproduce clonally and hardly produce any seeds (e.g. *Holcus mollis*).

Selective preservation of seeds is another factor that influences the relation between seed bank and former standing vegetation. Seeds that have adapted to long term dispersal through time have a higher chance of preservation than seeds of transient species (Cappers 1994). In addition, a distinction with standard seed bank ecology research is that in archaeobotany the seed residue, which is the remains of a germinated seed, counts as a unit as well, while for seed bank ecologists such a residue is of no value, e.g. for restoration purposes. As indicated, these kinds of uncertainties and deviations make the abundance-based analyses hard to value.

Concluding, it is important to keep in mind that seed bank contents and standing vegetation do not have a one-to-one relationship. Therefore, the reconstruction of former vegetation by interpreting seed bank data (or driftline material) should be based on existing recordings of seed banks and their standing vegetation for several community types. A substantial dissimilarity between seed bank and standing vegetation is often found. For example, Bekker *et al.* (2000) found Sørensen similarity indices between seed bank and vegetation data of dry and wet semi-natural grasslands between 40 and 60%. In addition, the seed bank and standing vegetation are also often quantitatively dissimilar across species.

The first analysis presented will be an environmental characterisation. Ellenberg indicator values for different environmental factors per species have been investigated which indirectly give information on the environmental conditions of the sites where the seeds have been found. Ellenberg indicator values exist for various ecologically important traits and factors. For each trait or factor of a certain species, the average value is generally used in the literature. It may, however, be informative whether a species has a broad or narrow ecological range, but this information is not derivable from the Ellenberg indicator values. Runhaar *et al.* (1987), instead, developed a similar scoring system which does include ecological ranges, but for this study the Ellenberg approach was chosen. This was because the fidelity-approach, described

below, enabled estimation of environmental conditions of a community type via assignment of certain high-fidelity species from the dataset to specific plant communities. For both the high-fidelity species as well as the specific plant communities, Ellenberg values or ranges can be defined which in a way give the same information as Runhaar's ecological ranges.

Following the environmental characterisation, species response curves have been drawn. A species response curve is a mathematical regression between soil seed bank data and standing vegetation data. This is primarily a methodological trial with the aim to use these relationships to estimate the abundance of species at the archeological site.

Next, fidelity-values have been gathered for all species of the archeological dataset. Each species occurs in a certain number of relevés from one or more community types. Fidelity-values indicate the percentage of the total number of relevés for which the species occurs in a particular community type. For example, a score of 87% for species X in community type A means that species X occurs in community type A in 87% of the total number of relevés in which species X occurs. The fidelity-values have been obtained from the SynBioSys database (Hennekens *et al.* 2001), a database containing ~450.000 vegetation recordings from The Netherlands which have computationally been labeled in a syntaxonomical, hierarchical system based on 2000 typical, pre-assigned community types.

Following, species coexistences have been investigated. The archeological dataset is limited and many species were probably present but have not been found in the archeological samples. In addition, it is unlikely that all species found belong to a single community type, so it would be worthwhile to pull the dataset apart in groups with species that strongly coexist within the group but not with species among groups. This has been tried by connecting those species which have coexistence values of 50% or higher. These groups, or rather networks, of species have been extended with species that did not occur in the archeological dataset, but which did have coexistence values of 50% or higher for species in the particular group. This would extent the database with species that probably were present in the area but have not been sampled. For this analysis, the coexistence values from the SynBioSys database (Hennekens *et al.* 2001) have been used.

Furthermore, a syntaxonomical approach was used to estimate to which plant communities the archeological data sets fit best. By using the SynBioSys database (Hennekens *et al.* 2001), the procedure was automated and yielded scores for goodness-of-fit. Also species groups based on the coexistence approach have been analysed.

A gradient analysis has been done on seed bank data from present brackish grassland, salt marsh, dry heathland, forest edge and riverine communities together with the archeological seed bank data to see where the archeological data fits in the multidimensional spectrum. Again, also species groups based on the coexistence approach have been analysed.

Finally, the species of the archeological dataset have been screened for shared seed traits which could explain their occurrence in the driftline material.

## METHODS, RESULTS AND DISCUSSION OF DIFFERENT APPROACHES

### ENVIRONMENTAL CHARACTERISATION

#### *Material and methods*

For each species found at the archaeological site, Ellenberg indicator values have been gathered for light requirement, soil moisture, soil reaction (acidity), soil nitrogen and salt tolerance (salinity). These values are adjusted for the area of The Netherlands and calibrated for soil analyses (Schaffers & Sýkora 2000). A principal component analysis (PCA) has been performed on this data of Ellenberg indicator indicator values belonging to different species to show patterns of variation in environmental needs for these species. Only those 15 species for which all used Ellenberg indicator values were present have been taken into account. The ordination was centered based on correlations between the unnormalized Ellenberg indicator values. PCA is generally used for ordination of environmental variables only (Kent & Coker 1995). The Eigenvalues calculated by PCA indicate the amount of variance that is explained by a certain axis.

Furthermore, overall average Ellenberg indicator values have been calculated as well as values for each of the three archaeological sites. In addition, since the sites lie on a slope towards a former creek, different subsets based on Ellenberg indicator values for moisture have been made and averages calculated for the other variables according to these subsets. Subsets are <7 and >7 for moisture values. The subset <7 ranges from dry to moist soil. The subset >7 ranges from moist soil to full water.

#### *Results*

Figure 5 shows the PCA graph with data from the 15 species for which all used Ellenberg indicator values were known. The most important variables are soil nitrogen, soil acidity and soil moisture, which have the longest arrows. Salt and light have less influence on the outcome. The Eigenvalues of axes 1 to 4 are 0.561, 0.286, 0.087 and 0.049, respectively. The cumulative variance therefore reaches a total of 98.2% for the first 4 axes.

The overall average Ellenberg indicator values (S.E.) for light, moisture, acidity, nitrogen and salinity are 7.3 (1.0), 7.7 (2.2), 6.5 (2.0), 6.6 (2.2) and 0.9 (2.1), respectively. The Ellenberg indicator values have been averaged for the species in the three samples taken in the excavations pits (Fig 6a). The light requirement of all species, whether overall or in the moisture gradient subsets, is relatively high. The plant communities need more than half-light conditions, usually in full light but at least 30% of full light. The soil moisture falls between 7 and 9, meaning that on average the species require a constant moist but not wet soil up to a totally wet, oxygen-poor soil. However, a substantial number of species require mesic to relatively dry soils, as can be seen from the subsets in Figure 6b. Soil acidity is on average neutral to a little acid, but is rather variable. Soil nitrogen content is preferably high but variable. The soil nitrogen demand is low but present in the mesic to wet subset of species but rather high for the mesic to dry subsets. The salt tolerance

is low but variable. Especially in the wet environment, salt tolerance is present in some species which increases the average salt tolerance. In the moist and light moist soils, salt tolerance is very low. Between the sites no significant differences in average Ellenberg indicator values could be detected.

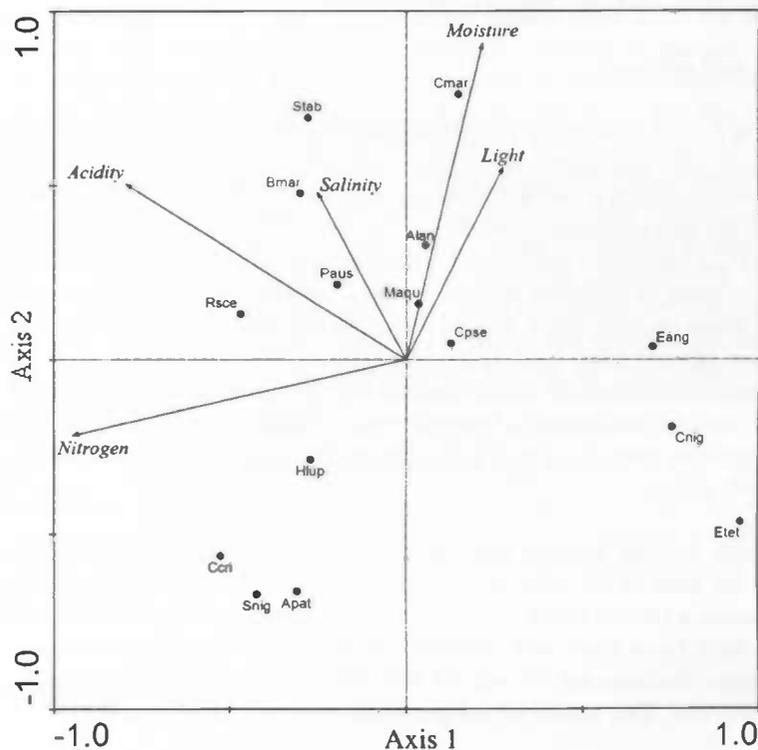


Figure 5. Principal component analysis of species and Ellenberg indicator values. Species names include the first letter of the genus and the first three letters of the species name. See Appendix A for archaeological dataset with full species names.

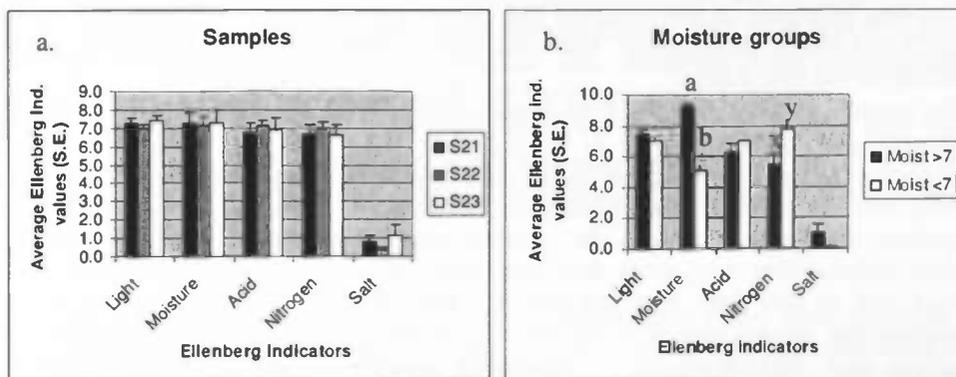


Figure 6. Means and standard errors of Ellenberg indicator values of light requirement, moisture, acidity and nitrogen content of the soil and salt tolerance for the three different samples (a) and for the different soil moisture groups (b). Letters *a* and *b* as well as *x* and *y* indicate significant differences.

Furthermore, Figure 6b shows the division between mesophilic (moisture <7) and hydrophilic (moisture >7) species, analysing the average Ellenberg indicator values in these two different classes of soil moisture in order to detect habitat characteristics of these two groups of species. Moisture value 7 did not occur in the database. Significant differences were found for the moisture and nitrogen groups by using a two-sided t-test assuming unequal variances ( $t_{18} = 12.1$ ;  $P < 0.001$  and  $t_{20} = -2.9$ ;  $P < 0.01$ , respectively).

### Discussion

On the basis of the PCA graph (Figure 5), a distinction can be made between a nitrophilous-aquaphobic group in the lower-left part, an acidophilic group in the upper-left part and an acidophobic group in the right part. The nitrophilous-aquaphobic group, consisting of *Solanum nigrum*, *Atriplex patula*, *Humulus lupulus* and *Carduus crispus*, possibly indicates an intermediately disturbed higher shore vegetation or it may be forest edge or bushy vegetation in an intermediate stage of succession. The high nutrient demand of these species may indicate human influence. The acidophilic-hydrophilic group consists of an acidophilic part with *Ranunculus sceleratus*, *Bolboschoenus maritimus*, *Schoenoplectus tabernaemontani* and *Phragmites australis*. This group is also slightly positively correlated with saline habitats. *Cladium mariscus*, *Alisma lanceolatum*, *Mentha aquatica* and *Carex pseudocyperus* are not correlated with acidity but rather with moisture and form the hydrophilic group. All species except *R. sceleratus* can be characterised as riverine species. The acidophobic group consists of *Eriophorum angustifolium*, *Erica tetralix* and *Carex nigra*. The position of the latter species is in contradiction with the fact that it is an acidophilic species, but maybe its nutrient-phobicity explains its position. *Erica tetralix* and *Eriophorum angustifolium* can be found in moist and nutrient-poor habitats.

Figure 6 shows rather high variances for the three archaeological samples, which resulted in the absence of any significant differences between the three archaeological samples. Thus, from the three samples, no specific environmental conditions can be deduced. However, the comparable averages may point to comparable contents of the driftline material. Because of this, it can be stated that the environmental conditions of the region are more or less homogeneous with respect to the contents of the driftline material, at least at the range investigated (~30 m) but probably also further. On a smaller scale, however, specific community types probably reveal more specific Ellenberg indicator values. Because of the comparability between the three samples, a grouping together of the samples is therefore not undesirable if this is advantageous for the analysis. In the Associa phytosociological approach, for example, the networks of co-occurring species have been built using the total list of species as if it occurred in one sample.

The light requirement of the species in the archaeological dataset is relatively high, indicating an open vegetation and/or low canopy as in grasslands, salt marshes and riverine communities (Fig 6a). The soil moisture is also relatively high, ranging from moist soils to aquatic environments poor in oxygen, but some species require relatively dry soils. Most species in the driftline material are therefore predicted to come from riverine and shore vegetations while some dry soil species may have been wind or water dispersed towards the creek. Some dry soil species, such as

*Chenopodium album* and *Polygonum aviculare*, are pioneers, which have a high seed production and high seed dispersal potential (r-strategists), explaining their presence in the driftline material. Acidity is on average neutral to weakly acid but variable. In present times, the weakly acid conditions would indicate rainwater influence, perhaps as run-off into the rivers that flow through the tidal creek system. However, at that time rainwater was not weakly acidic, so another reason must exist for this result, perhaps related to soil chemical properties. Nitrogen content of the soil is low in mesic to wet areas and high for the mesic to dry soils. It may therefore be possible that the drier areas are influenced by man. The farming practices, e.g. the keeping of cattle, but also the relatively high density of humans in the Swifterbant area, may yield in a high nutrient content of the soils, attracting specific plant species, such as *Urtica dioica*, *Rumex spp.*, *Ranunculus sceleratus* and *Carduus crispus*. Salinity is low but variable. Most species have a value of zero, being intolerable to salt, but some species have a low tolerance (*Bolboschoenus maritimus*, *Ranunculus sceleratus*, *Schoenoplectus tabernaemontani*) and others are truly halophytic or strongly tolerant (*Atriplex littoralis*, *Ruppia maritima*). The latter group of salt tolerant species explains the high variance of the overall group. The tolerant species are hydrophilic, while the intolerant ones grow on mesic to dry soils.

The division in two groups with Ellenberg moisture values of <7 and >7 yielded two significantly different groups, being moisture itself and nitrogen (Fig 6b). Again this shows that the mesic to dry soils (>7) contain species with a relatively high nitrogen demand, possibly indicating human influence, and that the riverine species demand a low nitrogen content.

## **SPECIES RESPONSE CURVES**

### **Material and methods**

Seed bank data and vegetation data from a variety of community types have been gathered (Table 2). The vegetation was scored on a dominance scale (1-4) (salt marsh data) or (recalculated) in percentage cover (other reference sites). For the seed bank data ten replicate samples were taken at two different depths, 0-5 cm and 5-10 cm, next to the plots. Corings were first sieved through a sieve with mesh size 0.212 mm and thereafter sown in boxes with sterilized soil. Seedlings were removed after identification. For details on the methods, see the references in Table 2.

For the species response curves, the upper and lower layer seed bank data have been summed. This was done because the actual archaeological data also consists of one value per species. Numbers of seeds have been  $\text{Log}_{10}$  transformed using the equation

$$Y = \text{Log}_{10}(X + 0.01)$$

in which X is the number of seeds and Y is its transformed value. Then, this data is used together with the dominance or percentage values to plot the seed-bank-to-vegetation data. SPSS (2003) was used to perform a curve estimation by using the option *Curve Estimation* under *Analyze > Regression*. The best fitting curve was chosen if it logically fitted the data points, with preference for the simplest relationship. The  $R^2$ -value and  $P$ -value was recorded and the species was scored as useful in vegetation description if the  $P$ -value was below 0.05.

**Table 2.** Reference sites, their community type, location, number of sites, number of relevés and reference to the data. The actual number of salt marsh sites is four, but recordings have been used from two different years. For the riverine vegetation, five sites have been used but at each site both riparian and water vegetation has been recorded and linked to the same seed bank data from the surface sediment on the bottom of the vegetated river banks.

Community type	Location	Sites	Relevés	Reference
Salt marsh	Schiermonnikoog NL	8 (4)	8	Chang, E.R. (2006)
Riverine vegetation	Twentekanaal NL	10 (5)	10	Boedeltje <i>et al.</i> (2003)
Lake shore	Zuidlaardermeer NL	2	20	Steendam & Bekker (2002)
Dry heathland	Various locations BE	11	42	Knevel <i>et al.</i> (2003)
Forest edge	Various locations BE	14	42	Knevel <i>et al.</i> (2003)
Brackish grassland	Uitkerkse Polder BE	3	30	Vanhecke <i>et al.</i> (in prep.)

## Results

Of all (348) species occurring in the reference seed bank datasets except the salt-marsh dataset, 12 species showed significant relationships between the standing vegetation and the soil seed bank (Table 3). A total of 9 other species showed significant relationships in a non-logical way and were left out of the list. Out of 12 salt-marsh species, 5 species showed significant relationships (Table 4). All species except *Spergularia salina* showed a positive relationship between seed bank and standing vegetation. The only species that is also present in the archaeological dataset is *Phragmites australis*. A graph of the relationship between seed bank and vegetation for *Juncus gerardi* is shown as an example (Figure 7).

**Table 3.** Species showing a logical significant relationship between standing vegetation and soil seed bank. Reference samples with vegetation recordings in percentage cover.

Species	R <sup>2</sup>	P	Relationship
<i>Alopecurus geniculatus</i>	0.251	0.020	Quadratic
<i>Eupatorium cannabinum</i>	0.159	0.013	Linear
<i>Juncus gerardi</i>	0.445	0.001	Linear
<i>Limonium vulgare</i>	0.089	0.007	Linear
<i>Lythrum salicaria</i>	0.364	0.001	Linear
<i>Phragmites australis</i>	0.674	0.000	Cubic
<i>Ranunculus repens</i>	0.290	0.028	Quadratic
<i>Spergularia media</i>	0.194	0.000	Quadratic
<i>Spergularia salina</i>	0.403	0.021	Quadratic
<i>Suaeda maritima</i>	0.456	0.000	Quadratic
<i>Tanacetum vulgare</i>	0.991	0.009	Cubic
<i>Typha sp.</i>	0.820	0.000	Cubic

**Table 4.** Species showing a logical significant relationship between standing vegetation and soil seed bank. Salt marsh reference samples with vegetation recordings in dominance scale.

Species	R <sup>2</sup>	P	Relationship
<i>Juncus gerardi</i>	0.588	<0.001	Quadratic
<i>Suaeda maritima</i>	0.456	<0.001	Quadratic
<i>Spergularia media</i>	0.194	<0.001	Quadratic
<i>Spergularia salina</i>	0.678	0.002	Linear
<i>Limonium vulgare</i>	0.089	0.007	Linear



archaeological sites and the obtained data compared to present-day seed bank compositions with accompanying vegetation recordings in order to be able to reconstruct the former standing vegetation.

## FIDELITY-VALUE APPROACH

### Material and methods

Fidelity-values, indicating the percentage of cases or the percentage of total cover that the species occurs in a certain community type, have been checked for all species of the archaeological dataset. The fidelity-values have been obtained from the SynBioSys database (Hennekens *et al.* 2001). Species with scores >50% have been noted including the community type they belong to.

### Results

Table 5 shows the species with a fidelity-value of >50% for a phytosociological alliance based on presence/(absence) and abundance. Table 6 shows for each of the suggested alliances the average Ellenberg indicator values for light, moisture, acidity, nitrogen and salinity. It should be mentioned that the Ellenberg indicator values for community types can be given based on species presence as well as on abundance, but the presented values based on presence do not differ remarkably from those based on abundance. Worth noting is that all alliances except Arction are related to wet environments.

Table 5. Species occurring in the archaeological dataset that have a fidelity value above 50% for a certain community type (code) with the number of diagnostic species and diagnostic species present in the archaeological dataset. The name of the diagnostic species is given where present.

Species	Fidelity	Alliance (syntaxon)	Diagn. spp.	Name of diag. spp.
<i>Ruppia maritima</i>	83.02	Ruppion maritimae (02AA)	2; 0 present	
<i>Cladium mariscus</i>	69.65	Caricion elatae (08BD)	2; 0 present	
<i>Atriplex littoralis</i>	68.97	Atriplicion littoralis (22AA)	1; 1 present	<i>A. littoralis</i>
<i>Conium maculatum</i>	53.33	Arction (31AB)	5; 0 present	

Table 6. Average Ellenberg indicator values for candidate alliances. L, light requirement; F, soil moisture; R, soil reaction; N, soil nitrogen; S, salinity.

Alliance (syntaxon)	L	F	R	N	S
Ruppion maritimae (02AA)	6	10	9	8	6
Caricion elatae (08BD)	7	8	7	5	0
Atriplicion littoralis (22AA)	8	5	8	7	3
Arction (31AB)	7	5	8	7	0
Average	7.0	7.0	8.0	6.8	2.3

## Discussion

Four different alliances have been found based on >50% fidelity of four species (Table 6). In the Ruppion maritimae (Figure 8) *Ruppia maritima* is a common species although not a diagnostic species for the alliance. It is however a diagnostic species for the association Ruppium maritimae. This association occurs in ephemeral waters which are protected from surges. The soil is clayey with high organic content. The vegetation withstands chloride concentrations from 0.5-8% and is even dependent on high summer chloride concentrations. In the Ruppium maritimae, *R. maritima* is very abundant together with two macro-algal species, which may explain why no other typical species have been found (SynBioSys; Hennekens *et al.* 2001). Therefore, it may be possible that this plant community type occurred at the archaeological site around 6000 BP. A total of 4 species found in the Ruppion maritimae alliance occurred in the archaeological dataset (8.5%).



Figure 8. An example of the community type Ruppion maritimae.

*Cladium mariscus* has a high fidelity in the Caricion elatae (Figure 9). The Caricion elatae is a sweet-water, terrestrialisation community in stationary water of peatland, dune valleys and old river arms. The soil is sandy or clayey but weakly nitrogenous. Apart from some *Sphagnum* species, *C. mariscus* is a very dominant species in this system, which explains its presence as seed at the archaeological site. Other highly abundant species with a high fidelity are *Carex paniculata* and *C. elata*, but these have not been found in the archaeological dataset. The two diagnostic species *Lysimachia vulgaris* and *Peucedanum palustre* have not been found either but also occur in a very low abundance which may explain their absence in the archaeological dataset. A total of 26 species from the archaeological dataset can be found in the Caricion elatae, which is 55%. These facts make it doubtful whether the alliance Caricion elatae occurred in the Swifterbant region. Furthermore, *Cladium mariscus* used to be far more abundant in the past than nowadays, which makes it more likely that it occurred in the Swifterbant area and ended up in the driftline material. However, its high abundance in the past make it also more likely that it occurred in other community types as well which do not occur anymore these days. If so, it will be hard

to reconstruct the community type in which *C. mariscus* could be found in the Swifterbant area, since this analysis is based on present day syntaxonomy. Thus, *C. mariscus* may not have been a very indicative species at the time of the Swifterbant culture in contrast to recent times.



Figure 9. An example of the community type *Caricion elatae*.

*Atriplex littoralis* is a diagnostic species of the alliance *Atriplicion littoralis* (Figure 10), or rather of its only association the *Atriplicetum littoralis*. *Atriplex prostrata*, *Elytrigia atherica* and *Matricaria maritima* are common species in this association (in decreasing order) although they have very low fidelities. These species do not occur in the archaeological dataset. The *Atriplicetum littoralis* is a typical coastal community growing for example on shorelines of tidal gullies in salt marshes. A total of 11 species found in the *Atriplicion littoralis* alliance occurred in the archaeological dataset, which is 23% of the species in the archaeological dataset. *Atriplex littoralis* is a hydrophilic species with a high nitrogen demand and a high salt tolerance. This is opposite to the findings of the environmental characterisation, which showed a division between hydrophilic species with a low nitrogen demand and mesic to dry species of meso- to eutrophic conditions. Perhaps *A. littoralis* grew near the settlement site where nutrient-rich water run-off occurred. It may also be a long-distance disperser coming from a more brackish to saline site far away.



**Figure 10.** An example of the community type *Atriplicion littoralis*.

*Conium maculatum* is a species with a high fidelity for the alliance Arction (Figure 11), a humus and ammonium rich, half-open to open community. The five diagnostic species were not present in the archaeological dataset, but it should be emphasized that the alliance consists of many species all with low presence and abundance. This makes it hard to determine whether this alliance actually existed at the Swifterbant site because the low numbers will make it unlikely that seeds will be caught. However, the alliance contains a total of 22 species from the archaeological dataset, which is 47% of all species found in the archaeological dataset. In addition, *Conium maculatum* is, according to basic archaeological knowledge, an indicative species for the so-called *zeedorpenlandschap*, or sea village landscape (Figure 12). It is an open landscape often present in the shelter of sand dunes where people affect their surroundings by means of extensive agriculture. This description fits with the topographical and cultural knowledge of the Swifterbant area.



Figure 11. An example of the community type Arction.

The Ellenberg indicator values from Table 6 will be compared with the average and partitioned Ellenberg indicator values for the archaeological species list (Figure 6). Light conditions of all alliances are comparable with the average and overall values from the archaeological data. Soil moisture, however, differs remarkably among alliances. The *Ruppion maritimae* and *Caricion elatae* need wet soil or open water whereas the *Atriplicion littoralis* and *Arction* demand mesic to dry soils. Such a division was also found in the archaeological dataset, because the driftline material consisted of species from wet as well as dry habitats. Average soil acidity of the alliances is higher than calculated from the archaeological data for most alliances. Furthermore, soil nitrogen demand is equal in the alliances and the archaeological dataset. Finally, salt tolerance demand is difficult to compare between alliances and groups of species as it is rather variable between species. This comparison shows that the alliances as appointed by the fidelity values result in more or less identical environmental conditions as the subset of species from the archaeological dataset. This strengthens these results.

It can be argued that circular reasoning plays a role in the comparison between the results of the environmental characterisation and the fidelity approach. The species having a high fidelity for a certain community type is often highly abundant in this community type. Therefore, the average Ellenberg indicator values of the whole community present the same values as those of the high-fidelity species alone. The high-fidelity species is also present in the environmental characterisation, so two overlapping analyses are compared.



**Figure 12.** An example of the 'zeedorpenlandschap', or sea village landscape, showing a little garden amidst the dunes overgrown by shrubs and grasses.

## ***SPECIES COEXISTENCE APPROACH***

### ***Material and methods***

The SynBioSys program offers data on coexistence of species (Hennekens *et al.* 2001). After choosing a species A, a list of other species with their percentage of co-occurrence with species A is given. All other species with a value higher than 50% occur in more than half of the relevés where species A is also present. The species of the archaeological dataset have been checked for co-occurrence. In this way, networks of interrelating species can be built. Also co-occurring species that do not occur in the archaeological dataset have been added to the networks.

### ***Results***

Figure 13 presents four smaller and larger networks (A, B/C, D and E) based on the coexistence values for species in the archaeological dataset. Four separate species (F, G, H and I) have been added on the bottom of the figure. These will become part of networks when species have been added which did not occur in the archaeological dataset (see Figures 17 and 18). Thorough descriptions of Figures 13 to 18 will be given in the discussion section. Figure 14 presents the extended version of network A, Figure 15 of network B/C and Figure 16 of D and E. The species in F and G are linked to the extended network B/C and the species in H and I have extended networks in Figure 17 and 18, respectively.

The networks extended with species not in the archaeological database have been used to upgrade the species lists with species "not found but probably present". The

list of extended networks contains *ruderal 1*, *ruderal 2*, *ruderal 3*, *wet 1*, *wet 2*, *wet 3* and *salt marsh*. The latter four groups have been left out of the gradient analysis since they contained too few species for proper ordination.

For each of the Figures 13 to 18, the arrows indicate the direction of the coexistence relation. The first number below the species names indicates with how many species from the archaeological dataset the actual species has a coexistence value higher than 50%. The second number below the species names indicates with how many species in general the actual species has a coexistence values higher than 50%. For the extension networks in Figures 14 to 18, the underlined species and dotted lines are extension arrows and species to the network, respectively.

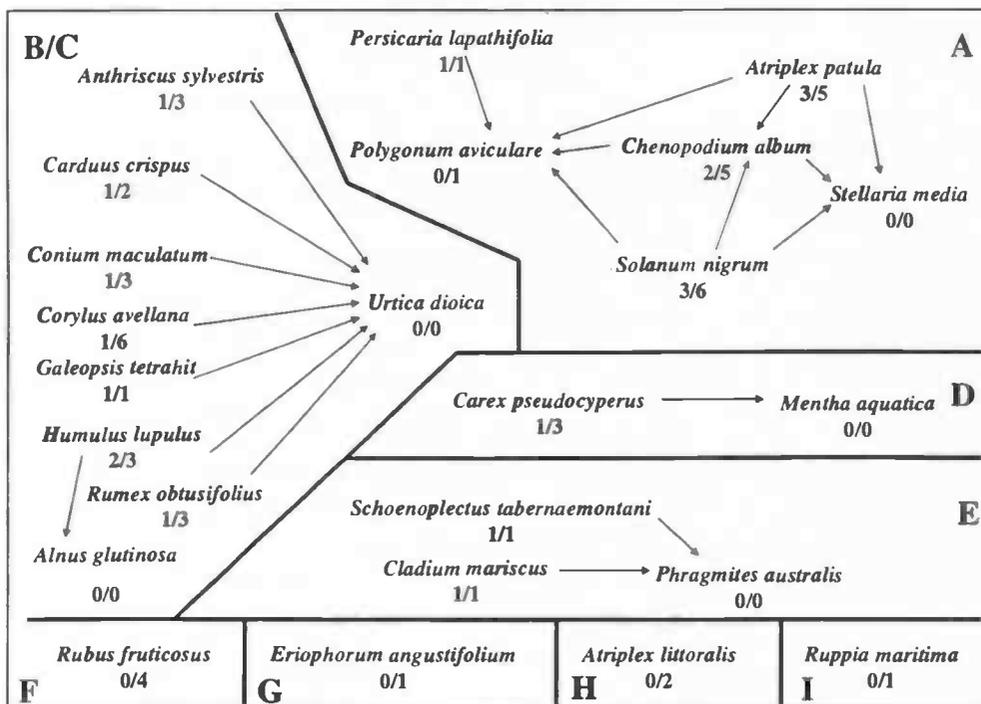


Figure 13. Species coexistence for species with probabilities >50% occurring in the archeological dataset.

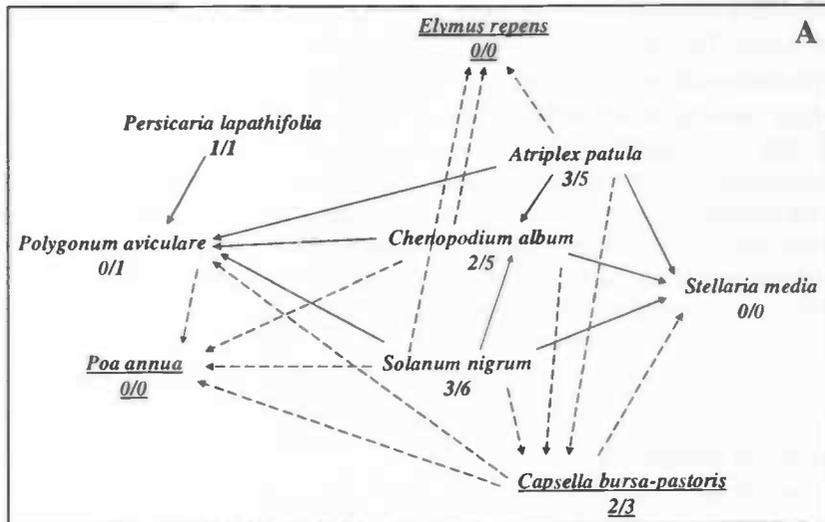


Figure 14. Ruderal 1 species group extended with the species not occurring in the archeological dataset. The network of >50% coexistence is closed and self-enforcing.

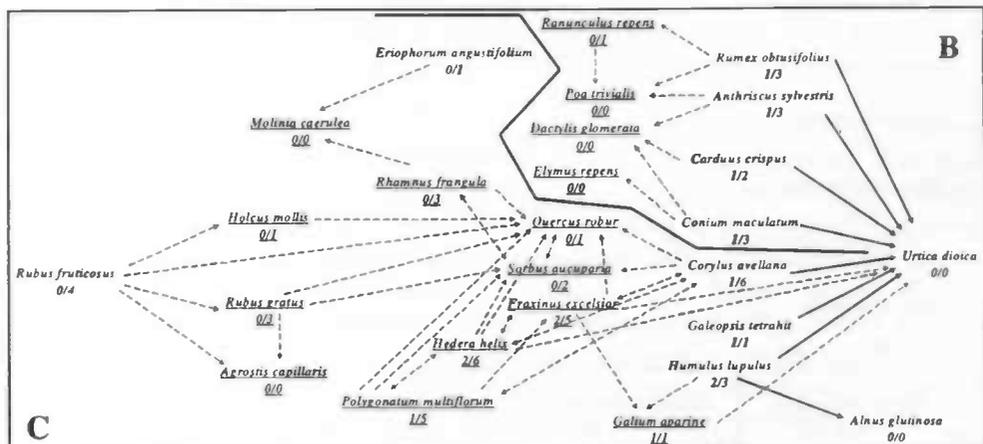


Figure 15. Ruderal 2 (B) and ruderal 3 (C) species groups extended with the species not in the archeological dataset. *Rubus fruticosus* (F) and *Eriophorum angustifolium* (G) have also been added to Ruderal 2 (C). The network of >50% coexistence is closed and divided in two sets of which the ruderal 2 (B) species group is semi-self-enforcing and the ruderal 3 (C) species group is strongly self-enforcing.



## Discussion

The environmental characterisation and the fidelity-value approach made clear that the archaeological dataset contains species from different community types. The species coexistence approach resulted in a separation of the dataset into four different groups. Figure 13 shows these four relationships between species based on their co-occurrence. The group on top, with *Chenopodium album* in its centre, consists of mesic, disturbed grassland species. It is called *ruderal 1* because of its high amount of pioneer species. The network on the left consists of nitrogen-demanding species which all coexist with *Urtica dioica*, a very common species. It can be described as an intermediate to late successional group and is called *ruderal 2/3*. The third (centre) and fourth (bottom) group consist of hydrophylic species, called *aquatic 1* and *aquatic 2* respectively. Concluding, this grouping argues in favour of the partitioning of the archaeological species list in different soil moisture groups.

These four networks have been fully extended with coexisting species that do not occur in the archaeological dataset. The disturbed grassland network *ruderal 1* remains a closed, highly interconnected group (Figure 9). *Ruderal 2/3* falls apart in two networks only connected via the common *Urtica dioica* (Figure 10). The upper part will be called *ruderal 2* and the lower part *ruderal 3* because the upper represents an intermediate successional stage while the lower represents a late successional stage with many woody species. Both networks remain intermediately connected. *Aquatic 1* did not extend tremendously and *aquatic 2* did not extend at all (Figure 11), possibly because these aquatic species are represented in communities with very different compositions so that they never co-occur significantly with other species. This is in sharp contrast with the ruderal species, which although common, co-occur strongly with other species. The fidelity-value approach did result in only one ruderal group (Arction) while the rest was aquatic. Aquatic communities may have more narrow ecological niches while ruderal communities have wider niches. Indeed, the co-occurrences shown in the networks are often unidirectional. This means that the network itself may consist of more than one community which are gradually connected to each other in the network. If all arrows were bidirectional, the case of one community type represented by the network would be much stronger.

Two extra networks could be built solely on *Atriplex littoralis* (Figure 12) and *Ruppia maritima* (Figure 13). Both networks are, however, not very strong since they are both based on only one species. *Atriplex littoralis* is rather unidirectionally connected to the whole salt-marsh group, but this connection is rather weak. *Ruppia maritima* is unidirectionally connected with three other species in the most simple network possible, which makes it not very probable that these other species did occur in the Swifterbant area.

## SYNTAXONOMICAL APPROACH

### Material and methods

The archeological macro-remains data have been imported as relevés into TurboVeg (Hennekens & Schaminée 2001) for the three different sites (S21, S22 and S23) using presence(/absence) data and seed abundance in relative percentages. In addition, the groups of species from the different networks obtained via the co-occurrence method (see above) have been imported in TurboVeg. Both networks with only those species found in the archaeological dataset as well as networks that have been extended with other co-occurring species have been imported. The SynBioSys module Associa was subsequently used to fit different datasets to plant community types (Hennekens *et al.* 2001). A fit-value has been calculated by summation of the 'normalised probability' and the 'exotic species value' given by SynBioSys to indicate the success of fit with a certain community type. The normalised probability is a chance value that the uploaded species list belongs to a particular community. The exotic species value affects this normalised probability negatively when the number of species that do not belong to the community type is high. The 'incompleteness' index, which Associa itself uses as a third factor to calculate its own fit-value, has been left out of the calculation used here. This was done because this factor, affecting the fit-value negatively with missing species, would have too much influence on the outcome since the archaeological datasets are likely to miss many species which naturally occur in certain community types. Fit-values at or below 1.0 indicate that the particular community fits the uploaded species list well. Negative values indicate very good fits, while values larger than 1.0 indicate bad fits.

### Results

Archeological datasets have been uploaded with seed abundance measured in relative percentages or with seed presence(/absence). The SynBioSys module Associa returned the first and second best fitting plant communities according to the calculated fit-values.

**Table 7.** Associa plant communities for archeological datasets for abundance and presence(/absence) data.

Dataset	First fit plant community	Fit	Second fit plant community	Fit
S21abun <i>n</i> =29	Echio-Melilotetum typicum (31CA01B)	1.8	Elymus repens-[Artemisietea vulgaris] (31RG04)	2.0
S22abun <i>n</i> =32	Elymus repens-[Artemisietea vulgaris] (31RG04)	2.0	Chenopodietum rubri roripetosum (29AA03C)	2.6
S23abun <i>n</i> =20	Chenopodietum rubri roripetosum (29AA03C)	1.8	Polygono-Bidentetum (29AA01)	2.4
S21pres <i>n</i> =29	Sileno-Tortuletum corynephoretosum (14CA02A)	9.2	Cladonio-Pinetum cladonietosum (41AA02A)	11.5
S22pres <i>n</i> =32	Cladonio-Pinetum cladonietosum (41AA02A)	12.8	Aira praecox-[Koelerio-Corynephoretea] (14RG02)	15.0
S23pres <i>n</i> =20	Aira praecox-[Koelerio-Corynephoretea] (14RG02)	9.9	Lysimachio-Caricetum aquatilis (08BC04)	11.0

Archaeological samples returned fit-values higher than 1.0 for abundance and presence(/absence) based analysis, indicating bad fits (Table 7). RG stands for *rompgemeenschap* which is Dutch for torso community. This indicates that such community types are remnants of other community types that probably existed at that location in the past, but which have deteriorated over time. Only diagnostic species

are still present, but highly abundant species are still belonging to the former community type. DG stands for *derivaatgemeenschap* which is Dutch for derivative community. Like a torso community, a derivative community type also contains the diagnostic species of the assumed former community type, but the highly abundant species are exotic to the former community type.

When using the unextended datasets for the four coexistence groups based on presence(/absence) data, Associa returned the plant communities listed in Table 8. The species of the extended networks based on presence(/absence) data returned from Associa the results listed in Table 9.

**Table 8.** Associa plant communities for archeological datasets for presence(/absence) data of coexistence groups. Fit-value based on lowest sum of 'Normalised Probability' and 'Exotic Species'.

Dataset	First fit plant community	Fit	Second fit plant community	Fit
Ruderal 1 <i>n</i> =6	Echinochloo-Setarium inops (30BB02B)	0.0	Pleurozium schreberi-Polytrichum formosum-[Vaccinio-Piceetea] (41RG01)	2.9
Ruderal 2/3 <i>n</i> =9	Philonotido fontanae-Montietum inops (07AA01D)	6.3	Potametum lucentis (05BA02)	6.8
Wet 1 <i>n</i> =2	Littorello-Eleocharitetum acicularis (06AD01)	-1.0	Charetum hispidac (04BA02)	-0.8
Wet 2 <i>n</i> =3	Charetum canescentis (04CA01)	0.8	Alismato-Scirpetum inops (08BB03D)	1.2

**Table 9.** Associa plant communities for archeological datasets for presence(/absence) data of coexistence groups extended with coexisting species. Fit-value based on lowest sum of 'Normalised Probability' and 'Exotic Species'.

Dataset	First fit plant community	Fit	Second fit plant community	Fit
Ruderal 1 <i>n</i> =9	Chenopodio-Oxalidetum fontanae (30AB03)	-1.3	Echinochloo-Setarium inops (30BB02B)	0.6
Ruderal 2 <i>n</i> =9	Riccietum fluitantis typicum (01AB01A)	11.2	Juncus effusus-Sphagnum-[Scheuchzerietae] (10DG01)	16.8
Ruderal 3 <i>n</i> =18	Rorippa amphibia-[Phragmitetea] (08RG02)	11.0	Philonotido fontanae-Montietum inops (07AA01D)	13.9
Wet 1 <i>n</i> =4	Littorello-Eleocharitetum acicularis (06AD01)	-0.7	Chara globularis-[Charetea fragilis] (04RG01)	2.5
Wet 2 <i>n</i> =3	Charetum canescentis (04CA01)	0.8	Alismato-Scirpetum inops (08BB03D)	1.2
Wet 3 <i>n</i> =4	Ruppium maritima (02AA01)	-0.5	Ranunculo fluitantis-Potametum perfoliati (05BA01)	-0.1
Salt-marsh <i>n</i> =15	Armerio-Festucetum litoralis (26AC02)	0.1	Puccinellietum maritima parapholidetosum (26AA01B)	0.1

## Discussion

The three datasets of the different subsites resulted in very high (i.e. insignificant) values with the Associa procedure for both abundance and presence based species lists (Table 7). Positive values around 2.0 were found for the abundance data and values around 10.0 were found for the presence(/absence) data. This indicates that the fit of the datasets to the suggested community types is not very good. The whole table is not regarded any further, since these high fit-values are probably the result of the mixture of plant species in the driftline material from different community types.

When the data were put together and split into groups defined by the >50% coexistence approach with only archaeological species, low values were found for most groups (Table 8). The ruderal species group 1 had a fit of 0.0; the ruderal species group 2/3 had a bad fit with 6.3. The aquatic species group 1 had a very good fit with -1.0 and the aquatic species group 2 had value of 0.8.

The datasets extended with coexisting species not present in the archaeological dataset revealed similar fit-values (Table 9). *Ruderal 1* had a value of -1.3 for a different

community type. *Ruderal 2* and *3* both had high fit-values around 11.0. *Wet 1* had a value of -0.7. *Wet 2* did not change its plant communities and corresponding fit-values of 0.8 and 1.2. The new *wet 3* had good fits with -0.5 and -0.1. The new *salt marsh* group did very well with 0.1 for the two best fitting plant communities.

Like in the fidelity approach, it can be argued that there is a circular reasoning when using extended network data. The extended networks contain extra species that have not been found in the archaeological dataset. The selection of these species is based on coexistence values which are derived from the same SynBioSys database which is used later on to calculate fit-values to community types. However, species that often co-occur together are likely to be present in the same community type(s). In this way, extending the networks with species that are likely to co-occur will probably increase the fit-values. This is exactly what happened with the early successional ruderal group. The other groups had comparable fits.

In the following, only the first fit plant communities with fit-values below 1 will be discussed. The three communities with negative fits for the extended networks are the *Chenopodio-Oxalidetum fontanae* (30AB03), *Littorello-Eleocharitetum acicularis* (06AD01) and *Ruppium maritimae* (02AA01). The *Chenopodio-Oxalidetum fontanae* often occurs in former-meadow arable fields in stream valleys. The soil should be moist and low in calcium and high in organic matter with a low to intermediate nutrient level. The high organic matter and low to intermediate nutrient level are new ingredients of the Swifterbant area. There are archaeological indications for the presence of cattle and agricultural practices, so (former-meadow) arable fields possibly existed. The species composition is in favour of this community. *Stellaria media*, *Poa annua*, *Capsella bursa-pastoris*, *Elymus repens* (three extension species) and *Chenopodium album* have high presence (>50%) in this community. However, no high abundance species (>25%) of this community type occur in the archaeological dataset, but that may be due to the high biodiversity of this intermediately disturbed community type.

The *Littorello-Eleocharitetum acicularis* can be found in standing water bodies which get periodically dry. The water should have a relatively high pH and the soil composition is variable although a small organic layer is present. It may be that this community occurred in the usually nutrient poor areas behind the levées which are protected against the tidal influence in the creeks, but which becomes flooded now and then. The name-giving indicator species, *Eleocharis acicularis* and *Littorella uniflora*, are absent from the archaeological dataset. In addition, no high abundance (>25%) species of this community type occur in the archaeological dataset. Of the species with presence in more than 25% of the community's relevés, only *Phragmites australis* and *Alisma plantago-aquatica* occurred in the dataset. This argues against the presence of this community type. It may be, however, that both the indicator species have characteristics making them avoid driftline material, but the absence of high

The *Ruppium maritimae* (or *Ruppium maritimae*) has already been described in the fidelity-approach section. The association occurs in ephemeral waters protected from surges. The soil is clayey with high organic content and the vegetation is salt-tolerant. Because this community type is species-poor of itself, it is difficult to estimate the probability that this community type occurred on the presence of only one species. Of

all archaeological species, only *Ruppia maritima* occurs often (>50%) and in high abundance (25%) in this community type. As said, the other high abundance species are algal species. It is thinkable that this association was present in the smaller creeks of the Swifterbant area. Since this species was also one of the indicator species in the fidelity approach, the good fit-value in the Associa approach can be assigned to that fact in addition to the fact that the extended species are likely to be present in the suggested community type due to high coexistence values (i.e. circular reasoning). Nevertheless, this does not prove against the existence of this community type; it should only be kept in mind that the methods that suggest this community type are not waterproof, especially when so few species support the *Ruppium maritimae*.

The three community types with fit-values between 0 and 1 are the *Echinochloo-Setarium inops*, *Charetum canescentis* and *Armerio-Festucetum litoralis*. The *Echinochloo-Setarium inops* occurs on nutrient-poor arable fields and consists of open pioneer vegetation with many ruderal species. The community type is well supported by the archaeological species, which is good evidence that is occurred in the Swifterbant area, although the name-giving species of this community type were absent. However, the extended network returned an even better fit with another but comparable community type.

The *Charetum canescentis* occurs in brackish waters with a sandy bottom. It contains a lot of *Chara spp.* which have not been found. This makes it not likely that the community type occurred, although it may be that *Chara spp.* does not end up in driftline material due to specific properties. The species from the archaeological dataset, *Phragmites australis*, plays only a minor role (33% presence, 3% abundance) in this community type.

The *Armerio-Festucetum litoralis* is a typical intermediate to high salt marsh community on sandy subsoil with some clay deposition on top. In grazed environments, this community type would turn into the *Juncetum gerardii*. The evidence for this community type is based on 15 plant species of which only one, *Atriplex littoralis*, occurred in the archaeological dataset but has an average occurrence of 2% in this community type with an average abundance of 2%. This makes it rather unlikely that this community type existed in the Swifterbant area.

To conclude the results, the first-fit community types which are supported by the Associa approach are the *Echinochloo-Setarium inops*, *Charetum canescentis*, *Chenopodio-Oxalidetum fontanae* and *Ruppium maritimae*.

The *Armerio-Festucetum litoralis* was excluded due to the fact that the archaeological dataset supported too few species. The *Charetum canescentis* was excluded because it contained only extended species except one. The *Littorello-Eleocharitetum acicularis* was excluded because the name-giving species were absent from the species list.

One community type has been found in both the fidelity approach and the syntaxonomical approach, being the *Ruppium maritimae* (02AA) based on the indicator species *Ruppia maritima*. The ecology of this community type has been discussed already. The fact that it appeared in different analyses argues in favour of the presence of this community type.

## GRADIENT ANALYSIS

### *Material and methods*

By performing an ordination on seed bank data from the reference sites (dry heathland, forest edges, brackish grassland, salt marshes, lake shore and riverine communities – Table 2) together with archaeological datasets, the relative position of the archaeological datasets to these specific community types can be observed. Detrended correspondence analysis (DCA) has been used to ordinate both log-transformed seed abundance and seed presence data from the seed bank of the reference sites with (1) the three archaeological samples separately and (2) the networks as produced with the coexistence approach, both (a) with only archaeological species and (b) with other co-occurring species. In addition, two datasets of Swifterbant, one old dataset of site S3 from Van Zeist and Palfenier-Vegter (1981) and one recent dataset of site S4 from Van Rooij (pers. comm.) from within the settlement, have been added to the presence/absence ordinations of the three archaeological samples (Appendix B). The DCA was performed using detrending by segments. Log-transformation for seed abundance data was performed using the equation

$$Y = \text{Log}_{10}(X + 1)$$

in which X is the number of seeds and Y is its transformed value.

Cultural species have been omitted from the archaeological datasets. For the reference datasets, when more than one species of a particular genus and a record with only the genus name were present in the datasets, the genus record was deleted. When one species and a record with only the same genus were present, the data of the species record was added to the genus record. For example, when *Arctium lappa* and *Arctium sp.* are present, the *Arctium lappa* record was added to the *Arctium sp.* record. As an exception to this rule, the data of *Taraxacum sp.* has been added to the data of *Taraxacum officinale* since this is the only species in this genus. Higher groups were all deleted, e.g. Apiaceae. CANOCO (Ter Braak & Šmilauer 1998) was used to produce ordination plots and to calculate the Eigenvalues of the axes.

### *Results*

The DCA graphs represent the relative positions of reference and archaeological samples. In the graphs, the notation 'Archaeological samples' indicates the three actual swifterbant samples. 'Early ruderal' means the species from the network of early successional ruderal species and idem dito for 'intermediate ruderal' and 'late ruderal'. Intermediate ruderal is only present in the extended networks graph, where the late ruderal is split up in intermediate and late groups.

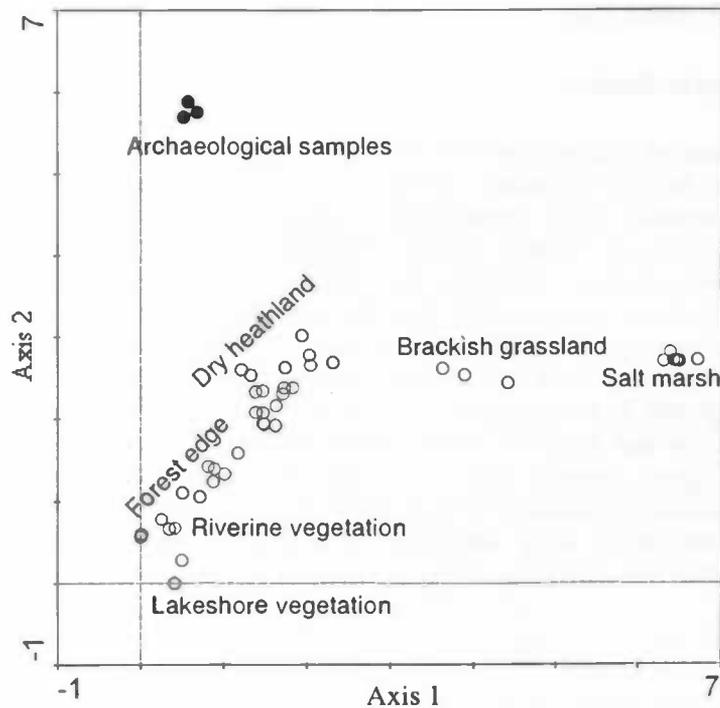
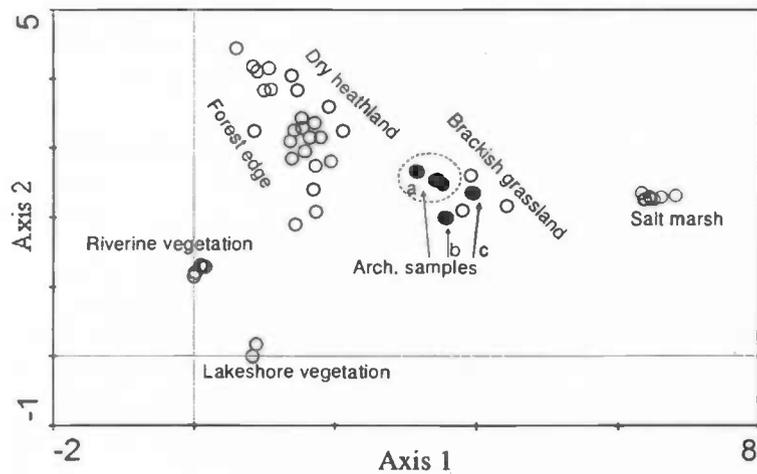
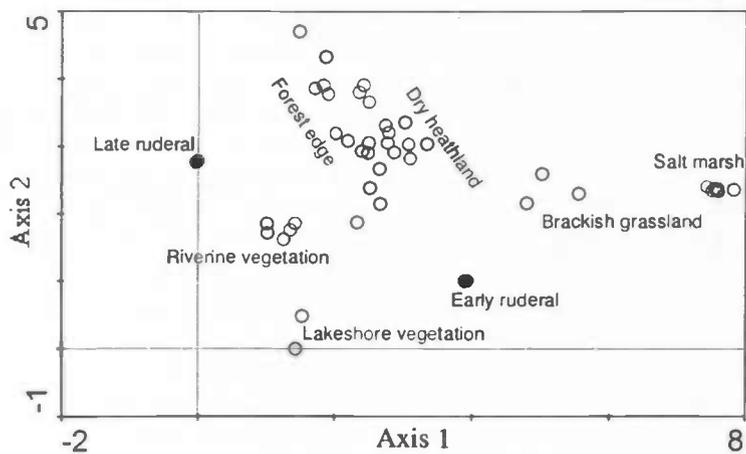


Figure 19. Log-transformed seed abundance data of reference samples (open circles) and archaeological samples (closed circles).

In the DCA of log-transformed seed abundance data (Figure 19) the archaeological samples show up far above the reference samples. The Eigenvalues of the first four axes are 0.868, 0.676, 0.293 and 0.248, respectively. In the same DCA procedure but with seed presence data instead of the seed abundance data, the archaeological samples end up mid-left of the brackish grassland samples (Figure 20). The Eigenvalues of the first four axes are 0.833, 0.462, 0.327 and 0.236, respectively. In Figure 21, the log-transformed abundance data of the archaeological networks turn up in between the brackish grassland and lakeshore vegetation for the early ruderal species group and to the left of the forest edge group for the late ruderal species group. The Eigenvalues of the first four axes are 0.868, 0.431, 0.266 and 0.199, respectively. The seed presence data of archaeological networks (Figure 22) shows a similar picture with the same relative positions for the early and late successional ruderal species groups. The Eigenvalues of the first four axes are 0.865, 0.445, 0.296 and 0.246, respectively.



**Figure 20.** Seed presence data of reference samples (open circles) and archaeological samples (closed circles). The three encircled samples are the actual Swifterbant samples. Two extra archaeological samples have been added, b, indicating the total species list from the excavation in Swifterbant S3 documented by Van Zeist & Palfenier-Vegter (1981), c, indicating the dataset from the recent excavation in the settlement area of site S4 by Jeroen van Rooij (pers. comm.).



**Figure 21.** Log-transformed seed abundance data of reference samples (open circles) and archaeological networks (closed circles). The early ruderal species group is situated between the brackish grassland sites and the lakeshore vegetation while the late ruderal species group is positioned on the outside left of the forest edge group.

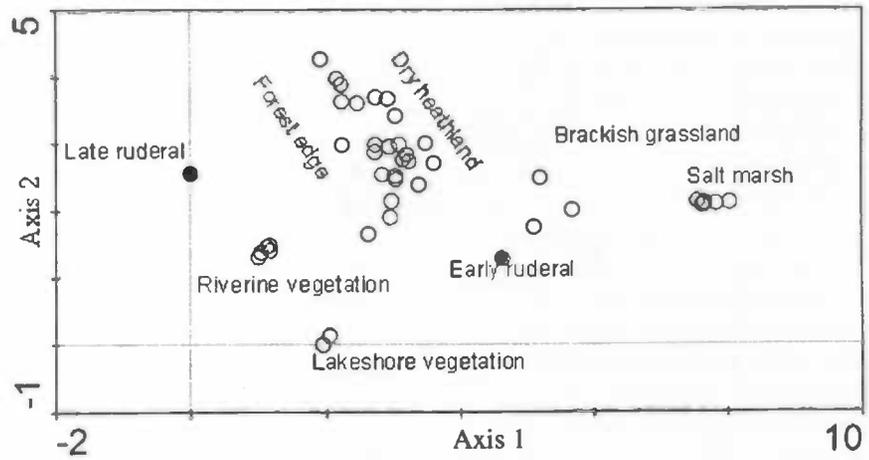


Figure 22. Seed presence data of reference samples (open circles) and archaeological networks (closed circles). The early successional ruderal species group is located between brackish grassland and lakeshore vegetation samples. The late successional ruderal species group is situated to the left of the forest edge samples.

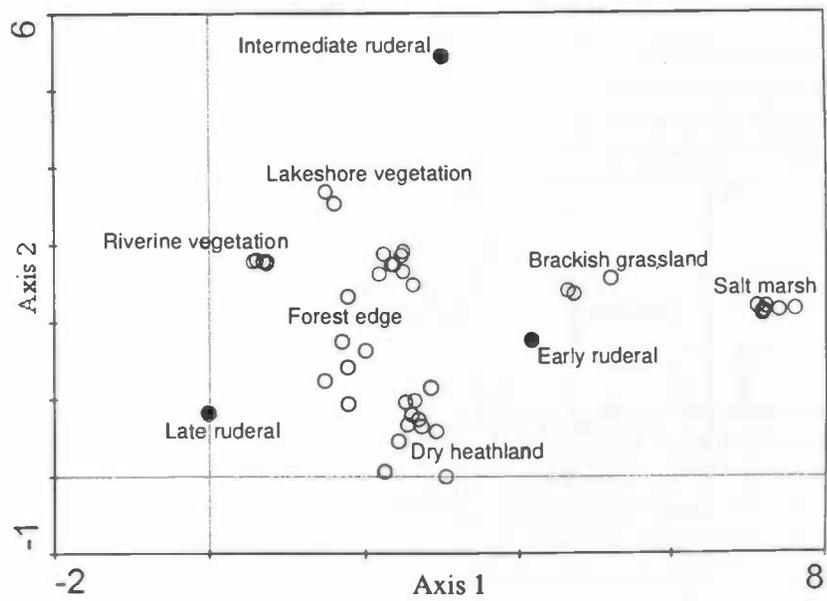


Figure 23. Seed presence data of reference samples (open circles) and extended archaeological networks (closed circles).

The seed presence data of extended archaeological networks (Figure 23) shows the intermediate ruderal group in between the early and late ruderal groups on a horizontal level but far above the reference samples in a vertical direction. Regarding the lakeshore and riverine vegetation samples, it seems as if the whole plot is mirrored horizontally. The forest edge and dry heathland samples are much more separated from each other than in the other graphs. The Eigenvalues of the first four axes are 0.865, 0.465, 0.286 and 0.230, respectively.

### *Discussion*

The first two axes of all ordinations explained substantial parts of the variation in the data. Most ordination graphs show identical groupings and relative positions of the groups. The salt-marsh samples are always located to the right. To the left of them, the brackish grassland samples are positioned and to the left of these, the dry heathland and forest edge samples are positioned, sometimes separated diagonally, sometimes mixed. Riverine vegetation is located to the left below the forest edge and dry heathland samples. The lakeshore samples are always located straight below the forest edge and dry heathland samples.

The first ordination axis is probably defined by salt tolerance, which extends from zero tolerance in forest edge species towards halophytic in the salt marsh. The second axis probably represents a moisture gradient extending from aquatic habitats in the lakeshore vegetation towards dry soils in the dry heathland. All ordinations show large ranges along the axes. This implies strong differences between groups of species. Also the variance explained by the first two axes is always high.

Both the reference and the archaeological samples were automatically grouped together according to vegetation type due to their similarity in species presence or abundance. Figure 19 shows the ordination of abundance data. The archaeological samples end up far above the dry heathland samples as if they share no single characteristic with the reference samples. According to the interpretation of the axes, the interpretation of this graph would be that the archaeological dataset consists of xerophilic species which is definitely false. In the other ordinations, the archaeological samples do not end up that far off, but often to the left of the Brackish grassland samples. Figure 20 is based on presence/(absence) data, and the archaeological samples including those of Van Zeist and Palfenier-Vegter (1981) and Van Rooij (pers. comm.) have been used which end up close to the Brackish grassland samples. But if the same ordination was performed with only the three archaeological samples from the actual study, they would end up on top again. This indicates that the group of three archaeological samples has too many absent species to end up close to the Brackish grassland samples. The samples of Van Zeist and Palfenier-Vegter and Van Rooij bridge the gap between the three archaeological samples and the Brackish grassland samples as they also contain many more species and therefore overlap with Brackish grassland samples much better.

Figure 21 shows the log-transformed abundance data with archaeological networks. The aquatic samples have been left out of the analysis because they contained too few species (2 & 3 species). The early ruderal (1) group ended up between the lakeshore vegetation and the brackish grassland vegetation, indicating it tolerates a low salinity and occurs on mesic soils in open vegetation. The late ruderal (2/3) group is positioned to the left of the forest edge samples. Keeping in mind the explanation of

the axes, the late ruderal group consists of salt-intolerant vegetation growing on mesic to dry soils. Figure 22, based on seed presence data with archaeological networks, shows exactly the same pattern.

Figure 23 shows the seed presence data with extended archaeological networks. At first sight it seems that the whole graph is plotted in horizontal mirror, with the lakeshore vegetation on top and the dry heathland below. The early ruderal group now ends up between brackish grassland and dry heathland, thus the three added species of *Poa annua*, *Capsella bursa-pastoris* and *Elytrigia repens* make the whole group more affinitive with drier areas (axis 2) although the low salt tolerance (axis 1) has been conserved. The new intermediate ruderal (2) group is positioned far above the lakeshore vegetation group, indicating a very wet environment for this group (axis 2). This is contradictory since the species making up this group are rather affiliated with mesic to dry soils. The late ruderal (3) group ended up a little drier (axis 2) than together with the intermediate species in Figure 22, between forest edge and dry heathland. Its salt tolerance is extremely low (axis 1). This may seem contradictory as well, since the extension of this group added a lot of tree species, which create a shaded, moister area compared to the intermediate ruderal (2) group. One would expect therefore the late ruderal (3) group to end up in a more moist area and the intermediate ruderal (2) group in a drier area. If the three ruderal groups represent a successional gradient, then the position of these three groups is logical since with succession, less influence of salt is expected as the succession can only proceed in higher elevated regions. The succession of lower elevations is halted by the influence of salt.

An explanation for the contradictory results found in these ordinations would be the interpretation of the axes. The salinity gradient of axis 1 seems to be right, but the moisture gradient gave problems. However, the extreme position of the intermediate ruderal (2) group in Figure 23 is hard to explain in any way, so it may be an artifact of the ordination procedure with these particular data.

## **SEED TRAITS**

### ***Material and methods***

In order to try to understand how the particular species of the archaeological dataset congregate in the driftline material, information on different seed traits has been gathered. Seed bank type has been taken from Thompson *et al.* (1997) as well as the number of long-distance dispersal (LDD) traits taken from Tamis (2005). Tamis discerned five different dispersal traits, being wind dispersal, water dispersal, (endo- and exo-)zoochory, dispersal by birds and dispersal by man. For some archaeological records (especially higher taxa), no long-distance dispersal traits were known. Other classes include 0 = no long-distance dispersal traits present, 1 = one long-distance dispersal trait present, 2 = two or more long-distance dispersal traits present.

## Results

The seed bank type and the number of long-distance dispersal (LDD) traits have been checked for the species of the archaeological dataset (Table 10). The same data have been summed in Figure 24.

**Table 10.** Seed traits of species from the archaeological dataset: seed bank type and number of long-dispersal traits. Sources are Thompson *et al.* (1997) and Tamis (2005).

Species name	Seed bank type	No. of LDD traits
<i>Alisma lanceolata</i>	-	1
<i>Alisma plantago-aquatica</i>	2	1
<i>Alnus glutinosa</i>	1	1
<i>Anthriscus sylvestris</i>	-	1
<i>Arctium sp.</i>	-	1
<i>Atriplex littoralis</i>	-	2
<i>Atriplex patula</i>	3	2
<i>Bolboschoenus maritimus</i>	2	1
<i>Carduus crispus</i>	-	1
<i>Carex nigra</i>	1	0
<i>Carex pseudocyperus</i>	-	2
<i>Chenopodium album</i>	3	1
<i>Cladium mariscus</i>	1	2
<i>Conium maculatum</i>	-	0
<i>Corylus avellana</i>	-	1
<i>Eleocharis palustris</i>	1	1
<i>Erica tetralix</i>	1	1
<i>Eriophorum angustifolium</i>	1	2
<i>Galeopsis tetrahit</i>	1	1
<i>Humulus lupulus</i>	1	0
<i>Malus / Pyrus</i>	-	2
<i>Mentha aquatica</i>	1	2
<i>Persicaria lapathifolia</i>	3	1
<i>Phragmites australis</i>	-	2
<i>Polygonum aviculare</i>	3	1
<i>Ranunculus sceleratus</i>	3	2
<i>Rubus fruticosus</i>	1	2
<i>Rumex obtusifolius</i>	2	1
<i>Ruppia maritima</i>	-	2
<i>Schoenoplectus tabernaemontani</i>	-	2
<i>Scirpus sp.</i>	-	2
<i>Solanum dulcamara</i>	-	2
<i>Solanum nigrum</i>	3	1
<i>Sonchus arvensis</i>	2	2
<i>Sonchus asper</i>	2	2
<i>Stellaria media</i>	2	2
<i>Typha latifolia</i>	3	2
<i>Urtica dioica</i>	2	2

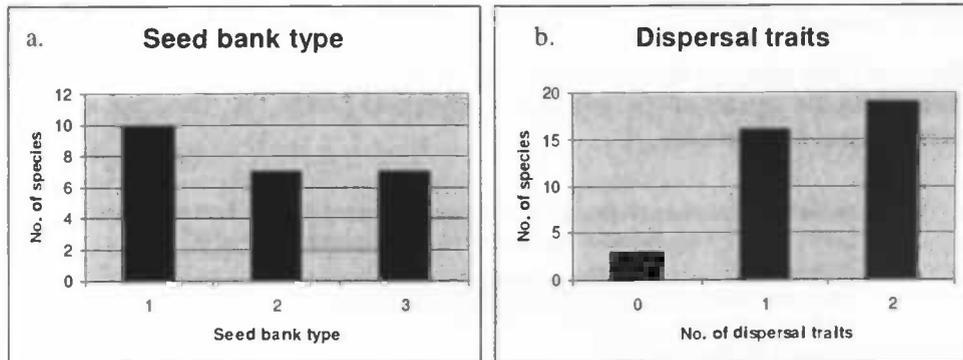


Figure 24. Seed bank type (a) and number of dispersal traits (b).

### Discussion

If the archaeological dataset was a true seed bank sample, one would expect to find predominantly long-term persistent species, since these species have optimized seed properties to successfully persist in the soil for a long time. However, the archaeological dataset used here consists of species that ended up in the sampled driftline material which do not predict a certain seed bank type to dominate the samples. This relatively equal distribution of seed bank types can also be seen in Figure 24a.

Figure 24b shows the number of long-dispersal traits which is expected to be high since this would increase the chance that it ends up in driftline material. Seeds of aquatic species probably have the potential for hydrochory, while the ruderal species are predominantly pioneer species which usually have high (wind) dispersal potential. In addition, these ruderal species would not have ended up in the driftline material if they did not have a high dispersal potential that could have brought them to the creeks by wind and then float with their feathery pappus on the surface of the water. This result can be seen in Figure 24b. The bar graph nicely shows that the largest group consists of species which have two or more long-distance dispersal traits, which is a common phenomenon but especially typical for species of open vegetation types (Ozinga *et al.* 2004). The ability to disperse by wind is often correlated with a long persistence in the seed bank by the fact that both abilities require a low seed mass. This would predict a high amount of long-term persistent species, but this was not what was found (Figure 24a).

## CONCLUSIONS AND FINAL DISCUSSION

### CONCLUSIONS

The Fidelity and Associa approaches resulted in a list of community types which may have existed in the Swifterbant area. Based on the discussion of these community types and their possibility considering the environmental characterisation and the gradient analysis, a final estimation of their likelihood is given (Table 11). If community types suggested by the phytosociological methods fit in the picture of the environmental characterisation and the gradient analysis, then its chance of occurrence in the Swifterbant area around 6000 yrs BP is well supported. Since each approach has its strengths as well as its weaknesses, the summation of the results may lead to good evidence for multiple supported community types and may rule out others which are badly supported by one or more of the approaches.

The Ruppion *maritimae*, or Ruppium *maritimae* in the Associa approach, was suggested by *Ruppia maritima* alone or with three extension species. As discussed above, this result is not strongly supported due to the methods used but the value of *Ruppia maritima* as an indicator species make the probability of the existence of this community type likely.

The Caricion *elatae* was not very well supported as other high abundant species and (low abundance) indicator species were absent from the archaeological dataset and because *Cladium mariscus*, the high fidelity species, was more abundant in the past and could therefore have occurred in other community types as well. It is also not fully supported by the gradient analysis as it needs a wet, fresh-water environment, which is not indicated by the position of the archaeological samples in the ordination graphs. This is strange since more than half of the archaeological species occurred in the Caricion *elatae*.

The Atriplicion *littoralis* gained a plus-minus for the environmental characterisation because it occurs in salt habitats with a high nitrogen content in the soil. This is contrary to the predictions of the environmental characterisation, which advocates either high salinity, wet, low nitrogen habitats or glycophytic, mesic to dry, intermediate to high nitrogen habitats. However, the variance in the averaged Ellenberg values was high and therefore the final assessment was given a plus.

The Arction was suggested by *Conium maculatum*. Because of absence of diagnostic species in the archaeological dataset, it is doubtful whether this community type occurred, although the environmental characterisation and the gradient analysis fit well with this community type (see *late ruderal* in Figure 21 & 22).

The only reason to exclude Echinochloo-Setarietum *inops* from the final list would be because the name-giving species of this community type were absent. However, the species of this community type are well supported by the archaeological dataset, and the environmental characterisation (although the nitrogen content may be somewhat low) and the gradient analysis are in favour of this community type.

The archaeological dataset lacked the name-giving indicator species of the Littorello-Eleocharitetum *acicularis* and any high presence and abundance species of this community type, which makes it unlikely that this community type occurred. Although it received plusses for the environmental characterisation and the gradient analysis, it received a minus in the final estimation.

The Charetum *canescentis* has been given a plus-minus due to the fact that many *Chara* species do not occur in the archaeological dataset. *Phragmites australis*, from

the archaeological dataset, plays only a minor role and cannot account for this community type.

The *Chenopodio-Oxalidetum fontanae* is very likely to have occurred, considering the species composition, the environmental characterisation (half-moist soil and intermediate nutrient level) and the gradient analysis (between brackish grassland and dry heathland for the extended network).

The evidence for the *Armerio-Festucetum litoralis* is very low, since 14 out of 15 species of the extended network species list are extension species. Therefore, this community type received a minus, which could not be compensated by the environmental characterisation and the gradient analysis.

**Table 11.** Community types as suggested by the Fidelity and Associa approaches. The F+A (Fidelity + Associa) column gives values to these community types according to their possibility to have occurred as discussed in the Fidelity and Associa sections. The EC column gives a value to the community types according to their possibility based on the results of the environmental characterisation. The GRD column gives a value based on the results of the gradient analysis. The TTL (total) column gives the final value considering the values given in the preceding columns.

Community type	F+A	EC	GRD	TTL
<i>Ruppion maritimae</i>	+	+	+	+
<i>Caricion elatae</i>	±	+	±	±
<i>Atriplicion littoralis</i>	+	±	+	+
Arction	±	+	+	±
<i>Echinochloo-Setarietum inops</i>	+	+	+	+
<i>Littorello-Eleocharitetum acicularis</i>	—	+	+	—
<i>Charetum canescentis</i>	±	+	+	±
<i>Chenopodio-Oxalidetum fontanae</i>	+	+	+	+
<i>Armerio-Festucetum litoralis</i>	—	+	+	—

Finally, it is possible to imagine a landscape inhabited by human beings around 6000 yrs BP in the Swifterbant area. Creeks and gullies traverse the landscape and fisherman span their nets between the sides at high tide, to catch the fish when it returns to deeper waters. On the edges of the creeks and gullies the *Atriplicion littoralis* and, in the more quiet parts, *Ruppion maritimae* grow in salt to brackish waters. More inland, where the rivers have more influence on the ecosystem, brackish creeks with reed can be found. Also behind the levées, brackish environments are probably found, perhaps with the *Caricion elatae*. Where cattle grazes, brackish meadows with low vegetation thrive. But there are also higher parts, where humans are more active. They might practice small-scale farming on the upper parts of the slopes of the sand dunes and creek levées. A *zeedorpenlandschap* can be envisaged, with the Arction, *Echinochloo-Setarietum inops* and *Chenopodio-Oxalidetum fontanae* as ruderal community types. On particular spots, man has chopped down the trees for timber and cleared the area of bushes so that houses could be built and arable fields could be created there, but on other sand dunes and levées shrubberies and trees remain. The presence of typical arable weed communities argues in favour of the presence of arable fields for production of cereal grains.

## **CRITICISM ON PHYTOSOCIOLOGY**

There has been much critique on the classification method of phytosociology (Ewald 2003). Continental researchers are often in favour of the phytosociological method, which assumes that there are distinct differences between vegetation types enabling classification of vegetation. The common critique on phytosociology comes from researchers in the Anglosphere who state that nature cannot be classified into distinct entities based on characteristics of the vegetation types themselves. Instead, they state that vegetation changes gradually and the only way to visualize and interpret differences is by means of gradient analysis. It is comparable to the debate between gradualists and punctualists on the nature of evolution.

In this report, both approaches, a classification approach and a gradient analysis, have been used. The drawback of the gradient analysis is that, although the relative position of the archaeological samples may come closer to the truth, it is hard to decide upon presence or absence of certain species in the prehistoric vegetation. The drawback of the phytosociological approaches has been explained already in that it is uncertain whether the community types that exist today did also occur in the past.

This is also central to the discussion about the tenability of the uniformitarian assumption (Cappers 1994). Behre and Jacomet (1991) state that uniformity in plant community types is valid for the whole Quaternary, but this statement can be doubted. For example, due to changing land-use practices over the centuries, the composition of weed and grassland associations have changed over time. But also the arrival of many neophytes in new areas throughout human history did not have neutral effects on vegetation composition (Alvarez & Cushman 2002).

## **SYNANTHROPIC VEGETATIONS**

The following species from the archaeological dataset are associated with human-influenced areas: *Urtica dioica*, *Polygonum aviculare*, *Polygonum lapathifolium*, *Chenopodium album*, *Stellaria media*, *Atriplex patula*. The same (and more) synanthropic species have been found by Van Zeist and Palfenier-Vegter (1981) in the settlement area in high abundance. It is thought that this is due to the dumping of these weeds in the settlement area to dry the soil, but ruderal vegetation types are also likely to have existed in and around the settlement.

The community types *Echinochloo-Setarietum inops*, *Chenopodio-Oxalidetum fontanae* and *Arction* can be characterized as ruderal community types, nowadays also occurring on or close to arable fields. These community types are usually dependent on intermediate disturbances, here probably brought about by human activities like farming practices and trampling of the vegetation.

It is worth mentioning the absence of *Juncus gerardi* in the archaeological samples as it is often mentioned as an important indicator of grazing. *Juncus gerardi* was present but not dominant in the samples from Van Zeist & Palfenier-Vegter (1981), but this may be due to the location of sampling, i.e. inside the settlement area. It is usually found in driftline material in brackish or salt environments and has a long-distance dispersal potential (Wolters & Bakker 2002). In the presence of grazers, other plant species of the high marsh are preferred by cattle, enabling *J. gerardi* to expand its range and turn the community composition into the *Juncetum gerardii* (Waterbolk 1976). However, it is a typical late-successional salt-marsh species, but like *J. gerardi* other typical salt-marsh species were absent as well. And the expected ungrazed, high

marsh associations (*Plantagini-Limonietum*, *Halimionetum portulacoides* and *Artemisietum maritimae*) have not been found in the phytosociological analyses. This is, therefore, a good explanation for the absence of *Juncus gerardi* in a grazed environment. It may be that the water in the creek was light brackish, enabling species which are salt intolerant or slightly tolerant to persist compared to high salt-tolerant species, creating brackish community types as found in this study.

#### **COMPARISON WITH VAN ZEIST & PALFENIER-VEGTER (1981)**

An important difference with the vegetation reconstruction performed by Van Zeist and Palfenier-Vegter (1981) is that in the present study different methodologies were devised beforehand in order to arrive at vegetation types in an objective manner, while the mentioned study used a more interpretative way based on the ecological knowledge of the researchers, in addition to a doubtful phytosociological approach. It is only in the discussion of the present study that the results of the analyses will be interpreted and valued on the basis of logical possibilities and probabilities, whereas it is unclear when Van Zeist and Palfenier-Vegter are discussing results or are still interpreting the dataset. The main problem in their publication is that suggestions are made which cannot or have not been proven. The authors focused on the finds, but they did not test these finds against a neutral background. For example, if *Conium maculatum* shows such a high abundance, one can argue that this is because it has been grown and used by the inhabitants for its medicinal properties. A good test to prove this would be to sample plant macro-remains in areas where no human settlement existed in the past and compare the abundances of *Conium maculatum*. Even then, the high abundance in the settlement area could have a natural cause or be explained as a statistical outlier. This is the clash between hermeneutics and empirism. Their phytosociological approach is based on the presence of species in the dataset that do also occur in the mentioned community types. On this basis they found the communities listed in Table 12. This table also gives information on whether the community types were found in this study as well. Some community types were indeed mentioned in both studies.

Furthermore, in contrast to the study by Van Zeist and Palfenier-Vegter (1981) the actual study is not based on macro-remains from inside a settlement area, but is more likely to represent the natural vegetation since driftline material has been sampled. However, the fact that this study concerns driftline material instead of seed bank material introduces another departure from an exact representation of the former standing vegetation.

**Table 12.** Community types predicted by Van Zeist and Palfenier-Vegter (1981) for site S3 based on their archaeological dataset and the occurrence of these community types at the class and alliance level in site S4 based on the syntaxonomical approach to the actual archaeological dataset. Community types with a question mark are doubtful due to name changes.

Community types site S3	Class found in S4?	Alliance found in S4?
Alno-Padion (38DG01)	No	No
Alnion glutinosae (39AA)	No	No
Salicion albae (38AA)	No	No
Molinietalia (12RG05)	No	No
Magnocaricion (08BC/BD?)	No	Yes
Scirpo-Phragmitetum (08BB?)	No	Yes
Scirpetum maritimi (08BB03?)	Yes	Yes
Potametea (05)	No	Yes
Ranunculo-Rumicetum maritimi (29AA02?)	No	Yes
Lolio-Plantaginetum (12AA01?)	No	No
Artemisietalia (26AC05?) (31?)	No	Yes
Polygono-Chenopodieta (29AA03?)	Yes	Yes
Sisymbrietalia (?)	No	No

The driftline samples are very localized in both space and time in contrast to the study performed by Van Zeist and Palfenier-Vegter (1981) who interpreted the combined dataset of a large area (316 m<sup>2</sup>) in several depth layers (6 times 10 cm). Of course it can be argued that the driftline samples are composed of material from a wide area, but this is probably even more true for the macro-remains found inside the settlement in the mentioned study since humans probably acted directly or indirectly as dispersal agents. The driftline material may be composed of macro-remains deposited over a longer time-span, instead of the assumption that it was deposited at once and perfectly conserved thereafter. In contrast to the mentioned study, it is unknown if and how long the driftline material was contaminated with macro-remains after its deposition.

### **FUTURE RESEARCH**

Driftline material is far from perfect for vegetation reconstruction, although it has some advantages too. Advantages are that one can be sure to find a high concentration of plant remains which are of local origin and that it is easy to estimate the age of the plant material by calibrated <sup>14</sup>C measurements (soil seed banks contain seeds of different ages, possibly over 100 years of age). Main disadvantages are that driftline material does not represent plant remains from only one plant community, that it contains mostly plant remains which are linked to riverine habitats (floating seeds etc.) and that (relative) abundances are hard to convert to abundances of standing vegetation (unless thorough investigations on driftline material will be done first).

Better would be to sample in the standardized way soil seed bank ecologists do, taking 10 corings of 10 cm depth and 4 cm diameter so that an area of 0.125 m<sup>2</sup> will be sampled per plot. The corings can be divided in an upper (0-5 cm) and lower segment (5-10 cm). Palaeological soil seed bank recordings can then be compared with the increasing number of recent seed bank recordings. When investigating seed banks of protohistoric (i.e. copper age to La Tène period for Northwestern Europe) or historic times, it would also be possible to take seed bank samples from palaeological sods of

dwelling mounds. On the basis of species presence, a community type should be assigned to the plot, whereafter the abundances and the relative amounts of seeds should be compared with data from present communities. Present communities should then be investigated in a similar manner, i.e. not by growing seeds in the greenhouse, but by sieving and counting seeds. In this way, the taphonomy (decay of plant remains) can be investigated, which will result in a factor to convert palaeologic samples to present-day numbers. Ideally, a curve can be drawn which links palaeologic figures to present-day figures for all plant species together, but it may very well be that taphonomy differs per plant species.

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## APPENDIX A – Raw data of archaeological samples S21, S22 and S23

The first column shows the species or higher taxa found. The second column shows whether the taxum has been used in the phytosociological analysis (and environmental characterisation) and/or the gradient analysis. The third column presents the plant part found and the last three columns give the number of occurrences the plant part has been found in sample S21, S22 and/or S23. The numbers indicate summed numbers of the plant parts, so 2 half seed parts are 1 whole seed. The indication 'cf.' has been ignored.

Species	Phytos. / Gradient	Plant part	S21	S22	S23
<i>Alisma lanceolatum</i>	1/1	seed		1	
<i>Alisma plantago-aquatica</i>	1/1	seed	1		
<i>Alnus glutinosa</i>	1/1	seed	3	2	
<i>Anthriscus sylvestris</i>	1/1	seed	1	3	
Apiaceae	0/0	seed		2	
<i>Arctium sp.</i>	0/1	seed	0	2	
<i>Atrilex littoralis</i>	1/1	seed	2		
<i>Atriplex patula</i>	1/1	seed	32.5	48	16
<i>Bolboschoenus maritimus</i>	1/1	seed	3	5	4
<i>Carduus crispus</i>	1/1	seed	3	1	
<i>Carex cf. pseudocyperus</i>	1/1	utricle		1	
<i>Carex nigra</i>	1/1	seed	2		
<i>Carex sp.</i>	0/0	seed	1		
<i>Chenopodium album</i>	1/1	seed	134	90	139
<i>Cladium mariscus</i>	1/1	seed	3	1	2
<i>Conium maculatum</i>	1/1	fruit	4	3	2
<i>Corylus avellana</i>	1/1	fruit		1	0.5
<i>Eleocharis palustris</i>	1/1	seed		6	
cf. <i>Erica tetralix</i>	1/1	leaf			1
<i>Eriphorum angustifolia</i>	1/1	seed	1		
cf. Euphorbiaceae	0/0				1
<i>Galeopsis cf. tetrahit</i>	1/1	fruit		1	
<i>Galium sp.</i>	0/0	seed			1
<i>Hordeum sp.</i>	0/0	fruit			0.25
<i>Hordeum vulgare sp.</i>	0/0	rachis		1	
<i>Humulus lupulus</i>	1/1	fruit		5	1
cf. <i>Lolium sp.</i>	0/0	floret		1	
cf. <i>Malus sp. / Pyrus sp.</i>	0/1	seed		1.5	
<i>Mentha aquatica</i>	1/1	seed	1		
<i>Persicaria lapathifolia</i>	1/1	seed	10	19.5	4.5
<i>Phragmites australis</i>	1/1	seed		1	
Poaceae 'tribe' triticeae	0/0	fruit		0.5	
<i>Polygonum aviculare</i>	1/1	seed	8	6	5
<i>Ranunculus sceleratus</i>	1/1	seed			1
<i>Rubus fruticosus</i>	1/1	fruit	1		
<i>Rumex obtusifolius</i>	1/1	seed		1	
<i>Rumex sp.</i>	0/0	seed	1		
<i>Ruppia maritima</i>	1/1	fruit			1
<i>Schoenoplectus tabernaemontani</i>	1/1	seed	9	5	12
<i>Scirpus sp.</i>	0/1	seed	1		
<i>Solanum dulcamara</i>	0/0	seed	3	1.5	
<i>Solanum nigrum</i>	1/1	seed	18.5	123	16
<i>Sonchus arvensis</i>	1/1	seed	1		
<i>Sonchus asper</i>	1/1	seed	1		
<i>Sphagnum sp.</i>	0/0		2	1	
<i>Stellaria media</i>	1/1	seed	18	7	6
cf. <i>Triticum turgidum ssp. Dicocon</i>	0/0	rachis		1	
<i>Typha latifolia</i>	1/1	seed	1		
<i>Urtica dioica</i>	0/0	seed	12	14	16
<b>Total</b>			<b>270</b>	<b>350</b>	<b>209</b>

## APPENDIX B – Raw data of archaeological samples of Van Zeist & Palfenier-Vegter (1981) and Van Rooij (pers. comm.)

The first and fourth column show the species or genus names. The second and fifth column indicate whether the species or genus occurred in the dataset from Van Zeist & Palfenier-Vegter (1981). The third and sixth column indicate whether the species or genus occurred in the dataset of Van Rooij. '1' is present, '0' is absent. See main text and reference for detailed information on these datasets.

Species	Van Zeist	Van Rooij	Species	Van Zeist	Van Rooij
<i>Alisma plantago-aquatica</i>	1	0	<i>Lycopus europaeus</i>	1	0
<i>Alnus glutinosa</i>	1	1	<i>Pyrus sp. / Malus sp.</i>	1	0
<i>Alopecurus geniculatus</i>	1	0	<i>Mentha aquatica</i>	1	0
<i>Anthriscus sylvestris</i>	1	0	<i>Menyanthes trifoliata</i>	1	0
<i>Arctium sp.</i>	1	0	<i>Moehringia trinervia</i>	1	0
<i>Artemisia vulgaris</i>	1	0	<i>Nymphaea alba</i>	1	0
<i>Aster tripolium</i>	1	1	<i>Oenanthe aquatica</i>	1	1
<i>Atriplex patula</i>	1	1	<i>Phragmites australis</i>	1	0
<i>Bromus mollis</i>	1	0	<i>Plantago major</i>	1	0
<i>Caltha palustris</i>	1	0	<i>Poa pratensis</i>	1	0
<i>Capsella bursa-pastoris</i>	1	0	<i>Poa trivialis</i>	1	0
<i>Carduus crispus</i>	1	0	<i>Polygonum aviculare</i>	1	1
<i>Carex disticha</i>	1	0	<i>Polygonum lapathifolium</i>	1	1
<i>Carex nigra</i>	1	0	<i>Polygonum persicaria</i>	1	0
<i>Carex paniculata</i>	1	0	<i>Potamogeton crispus</i>	1	0
<i>Carex pseudocyperus</i>	1	0	<i>Ranunculus acris</i>	1	0
<i>Carex riparia</i>	1	0	<i>Ranunculus ficaria</i>	0	1
<i>Carex rostrata</i>	1	0	<i>Ranunculus sceleratus</i>	1	1
<i>Carex serotina</i>	1	0	<i>Rosa sp.</i>	1	0
<i>Ceratophyllum submersum</i>	1	1	<i>Rubus sp.</i>	1	0
<i>Chenopodium album</i>	1	1	<i>Rumex conglomeratus</i>	1	0
<i>Chenopodium rubrum</i>	1	0	<i>Rumex hydrolapathum</i>	1	0
<i>Cirsium arvense</i>	1	0	<i>Rumex maritimus</i>	1	0
<i>Cladium mariscus</i>	1	1	<i>Salicornia europaea</i>	1	0
<i>Conium maculatum</i>	1	1	<i>Schoenoplectus tabernaemontani</i>	0	1
<i>Cornus mas</i>	0	1	<i>Scirpus lacustris ssp. lacustris</i>	1	0
<i>Cornus sanguinea</i>	1	0	<i>Scirpus maritimus</i>	1	0
<i>Corylus avellana</i>	1	1	<i>Scirpus tabernaemontani</i>	1	0
<i>Crataegus monogyna</i>	1	0	<i>Sium erectum</i>	1	0
<i>Eleocharis palustris</i>	1	0	<i>Sium latifolium</i>	1	0
<i>Galeopsis tetrahit</i>	1	0	<i>Solanum dulcamara</i>	1	0
<i>Galium aparine</i>	1	0	<i>Solanum nigrum</i>	1	1
<i>Galium palustre</i>	1	0	<i>Sonchus asper</i>	1	1
<i>Glyceria fluitans</i>	1	0	<i>Sonchus palustris</i>	1	0
<i>Hippuris vulgaris</i>	0	1	<i>Stellaria media</i>	1	1
<i>Hordeum vulgare</i>	1	0	<i>Trifolium repens</i>	1	0
<i>Hydrocotyle vulgaris</i>	1	0	<i>Typha angustifolia</i>	1	0
<i>Juncus articulatus</i>	0	1	<i>Typha latifolia</i>	1	0
<i>Juncus gerardi</i>	1	1	<i>Urtica dioica</i>	1	1
<i>Lapsana communis</i>	1	0	<i>Vicia sp.</i>	1	1
<i>Lychnis flos-cuculi</i>	1	0	<i>Zannichellia palustris</i>	1	0

