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# FACTORS INFLUENCING CHANGING AP/NAP RATIOS IN NW-EUROPE DURING THE LATE-GLACIAL PERIOD*

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RIASSUNTO - *Fattori influenzanti la variazione del rapporto AP/NAP nell'Europa nord-occidentale durante il Tradoglaciale* - Il Quaternario *Italian Journal of Quaternary Sciences*, 9(2), 1996, 599-604 - Nei depositi Quaternari della zona temperato-fredda dell'emisfero nord, la variazione del rapporto tra polline arboreo e polline non arboreo è spesso considerata indicativa delle temperature medie estive. Studi dettagliati di depositi Tardoglaciali in Europa nord-occidentale hanno mostrato che, oltre al tempo necessario per la migrazione dalle aree di rifugio, alcuni fattori diversi dalla sola temperatura possono avere determinato la mancanza di vegetazione arborea durante la prima metà del Tardoglaciale. Tali fattori tra loro correlati sono: condizioni oligotrofiche, bassa produzione di biomassa, iniziale assenza e conseguente basso contenuto di *humus* nei suoli ed un rapido processo di mineralizzazione dei già scarsi resti vegetali come conseguenza di temperature relativamente elevate. Inoltre, anche le incrostazioni che ricoprono il suolo e le sostanze tossiche prodotte dai Cyanobatteri possono avere inizialmente ritardato ed ostacolato l'immigrazione di alberi e lo sviluppo di una densa copertura vegetale. Un declino delle temperature estive durante l'Interstadiale Bølling-Allerød può avere innescato l'instaurarsi nel suolo di condizioni più favorevoli per la crescita degli alberi.

ABSTRACT - *Factors influencing changing AP/NAP ratios in NW Europe during the Late Glacial period* - Il Quaternario *Italian Journal of Quaternary Sciences*, 9(2), 1996, 599-604 - In Quaternary deposits from the cool-temperate zone of the N. hemisphere, the changing ratios of arboreal and non-arboreal pollen are often considered as being indicative for mean summer temperatures. Detailed studies of Late-Glacial deposits in NW-Europe have shown that – apart from time needed for migration from the refugia – some other factors than temperature alone may have influenced the lack of trees during the first half of the Late-Glacial period. Such inter-related factors were: oligotrophic conditions, a low biomass production, the initial absence, and the subsequently low content of *humus* in soils, and a fast process of mineralisation of the scarce plant remains as a consequence of relatively high temperatures. Also, soil covering crusts and toxic substances produced by Cyanobacteria initially may have delayed and hampered development of a dense herbaceous vegetation cover and the immigration of trees. A decline of summer temperatures during the Bølling-Allerød Interstadial may have triggered soil conditions that were more favourable for tree growth.

Keywords: Late-Glacial, AP/NAP ratios, palaeotemperatures, trophic conditions, Cyanobacteria.
Parole chiave: Tardo-glaciale, rapporto AP/NAP, paleotemperature, condizione trofiche, Cyanobatteri

## 1. INTRODUCTION AND DISCUSSION

Palynologists often used the fluctuations of arboreal *vs* non-arboreal pollen (AP/NAP ratios) in the cool-temperate zone of the Northern hemisphere to reconstruct changes of mean summer temperatures during the Quaternary (Van der Hammen *et al.*, 1967; Zagwijn, 1985). Zagwijn (1989) based estimates of mean July temperatures (°C) from pollen data on five assumptions. The first two assumptions are relevant for the Late-Glacial period: (1) Herb values of 50% approximate the northern forest limit when the total tree pollen is mainly *Betula* and *Pinus.* This limit coincides with the 10°C July isotherm. (2) The transition from *Betula* forest to pine-dominated forest runs roughly parallel to the July isotherm of 12°C.

In general, it is indeed correct to use the cognisance of present plant distributions and relationships between vegetation and temperatures as a yardstick. During periods with a mean summer temperature below 10°C, landscapes must have been treeless, whereas palynological evidence for the presence of trees indicates mean summer temperatures of at least 10°C. Additional variables which play a role in the relationship between climate and vegetation distribution are discussed by Prentice *et al.* (1992) and Huntley (1994).

The first generations of Quaternary palynologists already realised that, after a glacial period, trees needed time to migrate from their *refugiae* to new areas. For that reason Van der Hammen (1951) proposed that the *Artemisia*-rise at the beginning of the Late-Glacial period was a better indication of a rising temperature than the increase of tree pollen that only occurred centuries later, at the start of the Bølling *sensu stricto.* Nevertheless AP/NAP ratios were considered to reflect changing temperatures in the first place. The rather slow increase of arboreal pollen deposition during the first centuries of the Late-Glacial period was often interpreted as indicating a gradual rise in temperature (see, *e.g.,* Iversen, 1973, who stated "From no other period of such length as the Late-Glacial do we have such a detailed and reliable temperature curve"). However, during the 'Sixties' Russell Coope, after studying fossil Coleoptera (beetles) in British Late-Glacial deposits, concluded that a rapid climate change from cold to warm conditions had taken place around 13,000 BP. During the following 2,000 years data from fossil Coleoptera indicate an overall declining mean summer temperature. During the Younger

* Invited paper / *Comunicazione ad invito.*

Dryas (between ca. 11,000 and ca. 10,000 BP) the climate was sub-arctic. Late-Glacial Coleoptera records from the British Isles, Scandinavia and Poland are now available, and the value of fossil Coleoptera as sensitive indicators of past climates (Coope, 1986; Coope & Lemdahl, 1995) is generally accepted. Temperature curves based on ice-core data from Greenland show the same trends as Coope's temperature estimations based on fossil Coleoptera from the British Isles (Lowe *et al.*, 1995). Huntley (1994) used pollen-climate response surfaces and compared his pollen and macrofossil based palaeoclimate reconstruction for the Late-Glacial period of a site in Scotland with that of Atkinson *et al.* (1987), which was based on beetle remains. The results closely matched, with both studies indicating progressive cooling throughout the Late-Glacial interstadial. However, the studies disagree with respect to the extent of warming during the first centuries of the Late-Glacial period.

In the first instance most palynologists did not agree with Coope's ideas about the temperature development during the early part of the Late-Glacial. One could imagine that there was a time lag because trees needed time for migration (disequilibrium between terrestrial assemblages and climate; see Birks, 1986), but the idea that the warmest conditions occurred shortly after 13,000 BP was considered rather improbable. Kolstrup (1979; 1980) stressed the temperature indicator value of thermophilous aquatics and herbaceous taxa. An overview of factors influencing the migration of trees after a glacial-interglacial transition is given by Birks (1986). In the present paper some additional factors probably playing an important role after the sharp transition (ca. 13,000 BP) from glacial to interglacial conditions are presented.

## 2. THE STUDY OF THE LATE-GLACIAL DEPOSIT AT THE SITE USSELO

To tackle the problem of different temperature reconstructions in NW-Europe, Coope and Van Geel studied the Late-Glacial site Usselo, in The Netherlands (Van Geel *et al.*, 1984; 1989). A detailed study was made of microfossils (pollen, fungal spores, Algae, Cyanobacteria, etc.), macroscopic plant remains, and insects. The objective was to arrive at a single interpretation of changing climatic and local environmental conditions (*e.g.*, nutrient status, available humus, moisture conditions) in the coversand areas in NW-Europe. From the study of the deposit at Usselo it became evident that in the barren sandy landscape existing during the early part of the Late-Glacial Coleoptera were better temperature indicators than plant remains. The vegetation succession started in an oligotrophic pool with a very low organic production. The dominating factors for the vegetation succession during the 'Oldest Dryas' and the Bølling *sensu stricto* appeared to be the initially very low availability of nutrients, especially of N- and P-components. Also the absence of humus must have been an important factor because sand devoid of humus can become very dry in a short time, and many plant seedlings do not survive in such conditions (Pennington, 1986). During the early phase of the Late-Glacial period Cyanobacteria (formerly named Blue-green Algae) of the *Gloeotrichia*-type played an important role as pioneers at the aquatic sample site. Thanks to the nitrogen-fixing ability of these Cyanobacteria they opened up local conditions for other aquatic plants. Up to now Cyanobacteria were not recorded as recognisable fossils from dry sites, but it is highly probable that during the first half of the Late-Glacial they played a pioneer role in the Late-Glacial sand dunes. Terrestrial Cyanobacteria (*Oscillatoria, Microcoleus, Tychonema, Synechococcus, Lyngbya, Phormidium, Plectonema, Crinalium epipsammum*) can tolerate drought and intense solar radiation, and in recent sand dunes they act as initial colonisers by forming erosion-resisting crusts on the sand surface (Pluis & De Winder, 1990; Pluis, 1993; Roger & Reynaud, 1982). Such soil covering crusts may have formed a physical barrier for germinating seeds, especially when combined with the effects of toxic substances (disturbing the role of essential enzymes and inhibiting photosynthesis) that are produced by some Cyanobacteria (Abe *et al.*, 1996; Codd *et al.*, 1995; Kos *et al.*, 1995; MacKintosh *et al.*, 1990). However, at present cyanobacterial toxins are only known from aquatic taxa, such as *Lyngbya, Microcystis, Nodularia, Nostoc, Oscillatoria, Aphanizomenon* and *Anabaena* species (Carmichael, 1992; Skulberg *et al.*, 1984).

The presence of crust-forming Cyanobacteria may have hampered the formation of a dense stand of vegetation and the immigration of trees during the first centuries of the Late-Glacial period. In the present situation, eutrophication of sand dunes in NW-Europe is influenced by adjacent vegetation-covered areas (through animal droppings, transport of leaves and pollen) and by atmospheric deposition of N-components; and thus, colonization by herbaceous plants, and even trees, normally takes far less than a century (Gerlach, 1993; Olff *et al.*, 1994; Van der Maarel *et al.*, 1985; Van Dorp *et al.*, 1985). During the Late-Glacial however, the nutrient-poor sand dune area in NW-Europe was enormous in size. Enrichment in nutrients and humus derived from vegetation-covered areas was of minor importance and, as a consequence, processes of colonization by plants must have been much slower.

The reconstructed local and regional vegetation successions at Usselo show a slow increase of diversity which apparently was strongly influenced by the low level of nutrients at the start of the Late-Glacial. The sequence between 13,000 and 11,000 BP could be explained without proposing any cold climatic phase. The trophic situation and the groundwater level were apparently the important factors influencing the vegetational succession at the sample site. The situation at the start of the Late-Glacial was that of a barren sand dune landscape with damp sites and pools of water in the depressions. The most abundant beetles recorded after the start of the Late-Glacial at Usselo were (thermophilous) *Bledius* species, which make shallow burrows in damp sand where they feed on algae. During the first ca. 1,000 years of the Late-Glacial there was a gradual increase of diversity of the stand of vegetation, indicating a progressive eutrophication and an increasing organic productivity in the area, rather than an improvement of the climate (which already was warm since ca. 13,000 BP).

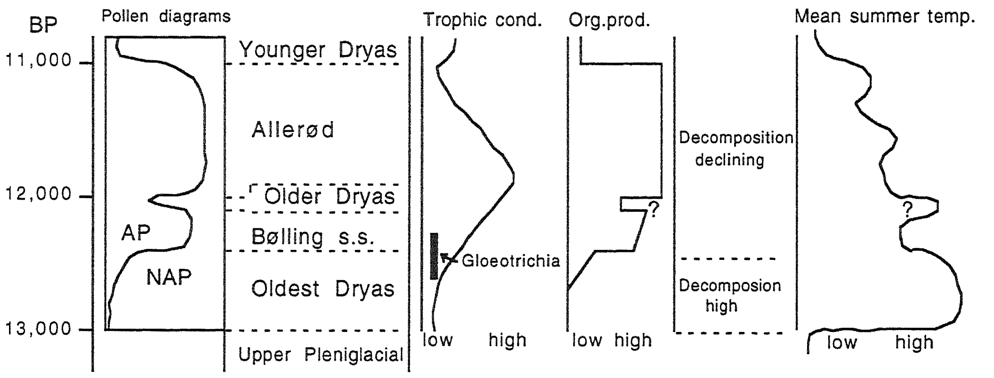


Fig. 1 - Probable Late-Glacial trends in sandy areas in NW-Europe can be summarised as follows: **Oldest Dryas:** Coleoptera indicate a sharp rise of temperatures around 13,000 BP, but tree pollen occurred in low frequencies for a period of at least half a millennium. Only a limited number of herbaceous taxa with a pioneer strategy could settle. The immigration of trees from their refugia occurred relatively slow, but probably the trees were also hampered in their immigration because of a very low level of nutrients, the initial absence of humus, low organic production and, in addition, the relatively high temperatures were responsible for a fast decomposition of the scarce organic material. Dry sandy soils which lacked humus and contained crusts of Cyanobacteria must have been difficult for trees to colonise. **Bølling *s.s.*:** The rising level of trophic conditions and also declining summer temperatures will have accelerated the net organic production (on account of less decomposition under a lower temperature regime), and as a consequence the accumulation of a humus component in soils increased. Soil conditions became suitable for the formation of a denser vegetation type with shrubs and trees. **Older Dryas:** It is not clear whether the decline of tree pollen deposition during the Older Dryas was caused by lower temperatures (for a discussion, see Van Geel *et al.*, 1989). Coleoptera data do not indicate a decline of summer temperatures that could cause birch trees to die, and from the ideas as mentioned above (see Oldest Dryas) it is even possible that the decline of tree pollen deposition during the Older Dryas must be attributed to a temporary rise of the summer temperatures that was unfavourable for Birches.Trophic conditions and biodiversity increased until the start of the Allerød period. **Allerød:** Soil-leaching processes in the sandy soils led to podzolisation and a strong increase of humus accumulation at the end of the Allerød period. There probably was a temperature decline and decomposition of organic material also may have been low as a consequence of the temperature trend. The spectrum of species on the poor podzolised soils declined in number. The landscape was covered with *Pinus-Betula* forest and with peat-forming vegetation in nutrient-poor conditions in the wet, low-lying areas. There is ample botanical, zoological and geological evidence that during the period of the Younger Dryas (ca 11,000 to 10,000 BP) sub-arctic conditions prevailed.

*I probabili* trend *Tardoglaciali nelle aree sabbiose dell'Europa nord-occidentale possono essere riassunti come segue:* ***Dryas Antico:*** *I Coleoptera indicano un brusco innalzamento delle temperature intorno a 13.000 BP, ma il polline arboreo è presente con frequenze basse per un periodo di almeno mezzo millennio. Solo un numero limitato di* taxa *erbacei con capacità pioniere può installarsi nell'area. L'immigrazione di* taxa *arborei dalle aree di rifugio avviene con relativa lentezza; probabilmente gli alberi sono ostacolati nella loro immigrazione dal livello molto basso di nutrienti e dall'assenza di humus. Suoli secchi privi di* humus *devono aver reso difficile la colonizzazione degli alberi. Nella sequenza acquatica del sito di Usselo la capacità dei Cyanobacteria di fissare l'azoto è di cruciale importanza per la successione vegetazionale. Probabilmente i Cyanobacteria hanno anche un ruolo importante come pionieri e colonizzatori iniziali delle superfici secche delle dune sabbiose. Le sostanze tossiche prodotte da tali Cyanobacteria possono avere ostacolato sia la formazione di una vegetazione densa che l'immigrazione di taxa arborei.* ***Bølling*** **s.s.**: *L'aumento del livello trofico ed anche la diminuzione delle temperature estive incrementano la produzione netta di sostanza organica (sulla base di una minore decomposizione in un regime di temperature più basse), e di conseguenza determinano un aumento della componente di* humus *nei suoli. Le caratteristiche del suolo divengono adatte alla formazione di un tipo di vegetazione più densa, con arbusti ed alberi.* ***Dryas Medio:*** *Non è chiaro se il declino della deposizione di polline arboreo durante il Dryas Medio sia stato determinato dalla diminuzione di temperatura (Van Geel* et al.*, 1989). I dati derivati dallo studio dei Coleoptera non indicano un declino delle temperature estive tale da determinare la morte della betulla e, per le considerazioni sopra menzionate (vedi Dryas Antico), è possibile che il declino della deposizione di polline arboreo durante il Dryas Medio debba essere attribuito ad un innalzamento temporaneo delle temperature estive che è risultato sfavorevole alla betulla. Il livello trofico e la biodiversità crescono fino all'inizio dell'Allerød.* ***Allerød:*** *Nei suolo sabbiosi processi di liscivazione portano a fenomeni di podzolizzazione e ad un forte aumento dell'accumulo di humus alla fine dell'Allerød. Probabilmente è avvenuta una diminuzione della temperatura, od anche il tasso di decomposizione del materiale organico può essere stato basso in conseguenza dell'andamento della temperatura. Il numero di specie sui suoli podzolici poveri diminuisce. Il paesaggio è coperto di foresta a* Pinus *e* Betula, *con vegetazione torbigena in condizioni povere di nutrienti nelle aree basse ed umide. Esiste un'ampia documentazione di carattere botanico, zoologico e geologico che indica come durante il periodo del Dryas Recente (circa da 11.000 a 10.000 BP) prevalgano condizioni sub-artiche.*

This development of the vegetation cover is paralleled by an increasing diversity of the insect fauna. Shortly after the start of the Allerød period the tendency towards eutrophication at the sample site ended when open water became filled up with vegetation and, once a peat deposit was formed, the local vegetation lost its contact with the groundwater and conditions gradually became oligotrophic to ombrotrophic.

The availability of humus in soils depends on biomass production, but also on the rate of decomposition and mineralisation which is influenced by, among other factors, the temperature. Recent studies by Walker *et al.* (1993) at the British site Gransmoor indicate that the increase of tree pollen at the start of the Bølling *s.s.* coincided with a decline of temperature (as based on Coleoptera-data). If temperatures indeed were the highest shortly after 13,000 BP, then the scarce plant remains were decomposed so quickly that humus could hardly or not be built up. A declining temperature at the start of the Bølling *s.s.* may have been an important trigger for the start of humus accumulation (through less decomposition) in the surface layer of the soils. This development may have been responsible for the increase of *Betula* and *Juniperus* which characterises the start of the Bølling *sensu stricto.* Figure 1 shows the trends of the different factors that probably played a role in the development of soils and vegetation in sandy areas in NW-Europe and a short overview is given of the development between ca 13,000 and 11,000 BP.

## 3. CONCLUSION

In the NW-European Late-Glacial forest history the temperature factor probably was misunderstood and the migration time factor probably was overestimated by palynologists. If factors like oligotrophic conditions, initial absence of humus, and the presence of crusts and toxic substances of Cyanobacteria indeed played an important role, then the supposition of a 'time-lag' (Coope, 1977 and pers. comm., 1995) in the response of the vegetation to deglacial warming is probably a misconception: the above-mentioned edaphic factors may have been limiting factors for tree growth, by dominating over the temperature factor. A decline of the summer temperatures at the start of the Bølling *s.s.* may even have triggered the accumulation of humus and the development of *Juniperus-Betula* pioneer forest.

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