The spread of bread wheat over the Old World since the Neolithicum as indicated by its genotype for hybrid necrosis.

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Summary: the spread and distribution of bread wheat in the Old World (Europe, Asia, Africa) since the Neolithicum as shown by the distribution of two necrosis genes and their alleles was studied. As basic material 1130 bread wheat landraces were investigated. Based on this distribution the routes by which bread wheat migrated are shown. The spread was done by migrating farmers and by farmers handing over seed to neighbours.

Abstract in French on page 46.

The cultivation of wheat is one of the more common agricultural activities depicted in medieval calendars. Attributed to Jean Le Noir (French, active 1331–75). *The Prayer Book of Bonne of Luxembourg, Duchess of Normandy* (detail), before 1349. Made in Paris, France. French. Tempera, grisaille, ink, and gold on vellum; Overall (closed): 5 3/16 x 3 13/16 x 1 5/8 in. (13.2 x 9.7 x 4.2 cm) Overall (approx. size opened): 5 3/16 x 7 11/16 x 2 13/16 in. (13.2 x 19.5 x 7.1 cm) Individual folios: 4 15/16 x 3 9/16 in. (12.6 x 9 cm) Storage (Book Box): 6 5/16 x 5 3/16 x 2 3/8 in. (16 x 13.2 x 6.1 cm). The Metropolitan Museum of Art, New York, The Cloisters Collection, 1969 (69.86)

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THE SPREAD OF BREAD WHEAT OVER THE OLD WORLD SINCE THE NEOLITHICUM

AS INDICATED BY ITS GENOTYPE FOR HYBRID NECROSIS

par A.C. ZEVEN*

1. INTRODUCTION

1.1. GENETIC SYSTEM OF HYBRID NECROSIS

Although VAVILOV in his publications had already described «albino» F_1 plants, DEKAPRELEVICH (1930) probably was the first to publish about hybrid necrosis. The «albino» F_1 plants may have been necrotic, but there are more genetic systems underlying similar weaknesses of hybrids. The second person to report on hybrid necrosis is perhaps KOSTYUNCHENKO (1936). He described a genetic system which showed the presence of complementary genes. At that time no further genetic research could be done in the USSR, but elsewhere research-workers and breeders had also encountered this phenomenon and investigated it. HERMSEN (1962, 1963 a) summarized the literature and recapitulated his own research work. He established two genes Ne_1 and Ne_2 and a multiple allelic series for each of them, namely

$Ne_1 : ne_1, Ne_1^w, Ne_1^m, Ne_1^s$ (w: weak, m: moderate, s: strong);

$Ne_2 : ne_2, Ne_2^w, Ne_2^{mw}, Ne_2^m, Ne_2^{ms}, Ne_2^s$.

Names were introduced. So, a variety with Ne_1 is called and Ne_1-carrier and one with Ne_2 an Ne_2-carrier. A variety without an Ne-allele a non-carrier.

1.2. SOURCES OF NE-GENES.

HERMSEN (1962, 1963b) also studied the distribution of the mentioned Ne-alleles among the varieties and established for several related groups of

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varieties the original source of the Ne-allele. Thus he found $Ne_1{}^s$ in several durum varieties, and discovered that $Ne_1{}^s$ in most of the bread wheat varieties (*T. aestivum/compactum*) had been incorporated through Marquillo. This variety is a cross of Marquis bread wheat (non-carrier) x Iumillo durum ($Ne_1{}^s$-carrier). Due to lack of old varieties at that time it was not possible to establish the original source of $Ne_1{}^m$ in many German varieties and of $Ne_1{}^w$ in many Belgian and also in many Australian varieties. The $Ne_1{}^w$- allele of Italian varieties originated from the Italian local wheat Rieti.

Five main sources of Ne_2 have been identified. They all have a European origin. These sources are :

1. Squarehead (of unknown source),
2. Noé (a French «local» wheat, originally introduced from Odessa, USSR),
3. Mediterranean wheats of the USA,
4. Crimean wheats of the USA and
5. Barleta, an Argentinian local wheat believed to have been introduced from Spain.

This last group could be extended to include Brazilian local wheats, which probably also came from the Iberian peninsula. In fact, these five groups could be reduced to :

1. Crimean and Ukrainian wheats, including the so-called Mediterranean wheats,
2. Iberian wheats including those from South America, and
3. Squarehead, of unknown origin.

1.3. GEOGRAPHICAL DISTRIBUTION OF CERTAIN CHARACTERISTICS

Ne-genotypes : From data published by HERMSEN (1962, 1963a, 1963b) and other workers (ZEVEN, 1965) and from unpublished data, a preliminary study of geographic distribution of the Ne_1- and Ne_2-alleles was made (ZEVEN, 1966). Ne_1 occurs south of the Mediterranean - Black Sea - Lake Baykal belt : north of this Ne_2 is found; ne_1 and ne_2 are discovered everywhere. In a postscriptum to this paper on the geographic distribution a publication by TSUNEWAKI & NAKAI (1965) was discussed. These authors has observed that Ne_1 occurred in the whole of Japan, whereas Ne_2 was restricted to the northern part. They suggested that the Ne_2-carriers were introductions from Europe and the USA. ZEVEN (1966) argued that these also could have come from Siberia. Later TSUNEWAKI et al. (1971) concluded that about 30% of the Chinese wheat varieties were Ne_1-carriers and that this frequency was preserved in common wheat during its eastward dispersion from Central Asia through China to Japan. They also found Pakistani, Afghanistani and Iranian wheats to carry Ne_1, but not Ne_2. This agrees with the above division into an Ne_1-area and an Ne_2-area. Similarly to our work, TSUNEWAKI c. s. investigated the distribution of Ne-genes. The use of their results is limited in great measure, since :

1) no attention is paid to the distribution of the alleles,

2) modern varieties are included, which blurs the picture, and
3) varieties are considered as being native while in fact they are exotic.

Thus varieties from Germany carrying Ne_1s or Ne_1^m were included, though these alleles are exotic to the German varieties and have entered them in recent times through Marquillo (from USA) and Garnet (from Canada). The same is true where Ne_2-carriers are concerned.

When, not so long ago, Mexican wheats were introduced on a large scale into India, an extensive introduction of Ne_2 into this Ne_1-area took place. Among varieties described by TSUNEWAKI c. s. as Russian four came from China, three from Poland, two from India and one from each Finland, Pakistan, Mongolia and Nepal. So 13 varieties in all were wrongly classified. More examples are given by ZEVEN (1969, 1976). The data from TSUNEWAKI c. s. should therefore be used with care. The above literature on Ne_1 and Ne_2 carriers and other pertinent publications have been summarized by ZEVEN (1967-1976).

Other characters : an earlier attempt to divide the wheats of the Old World into geographical groups was made by FLAKSBERGER c. s. (1938). They found two main groups :

1. The Indo-European wheats occurring in Europe (except the Mediterranean regions), the Far-East, Manchuria, part of China and Japan.
2. The Irano-Asiaticum wheats found in Anterior Asia, Central and SW Asia, Mediterranean countries, the Indian subcontinent, Africa and part of China.

In a later stage it will be seen whether this division coincides with the distribution of Ne-alleles.

ZEVEN (1970) used the genotypes for hybrid dwarfness (HERMSEN, 1967) of local wheats to study the geographical distribution of the dominant alleles of three D-loci. He found that gene D_1 occurs in southern Europe, Africa and Asia, gene D_2 in all wheat areas and that gene D_3 is confined to Europe. FROST & HOLM (1977) investigated the flavonoid patterns of 83 primitive spring wheats. This number is too small to discover any geographical distribution of certain flavonoids.

GOTOH (1979) found that spring habit in indigenous Japanese varieties was conditioned by gene Vrn-3. This gene is also identified in Chinese Spring (PUGSLEY, 1972). This would mean that this gene could be used as a marker gene to establish the relationship of local varieties of wheat in (East) Asia and therefore testing local varieties of spring wheat from that region for this gene should be continued.

2. *METHODS*

In the first years completely fertile Ne_1^s- and Ne_2^s-carriers were used as testers for the varieties to be investigated (see 3. Materials); from 1966 onwards *timopheevi*-cytoplasmic male sterile testers were used. F_1-grains were sown in pots; the seedlings were transplanted into the field and later into the green-house. The F_1-plants were scored for their degree of necrosis. Applying HERMSEN's (1962, 1963a) criteria, the strength of the alleles was established.

Because male sterile tester lines were used, F_2-plants could be obtained and grown only if the tested variety carried Rf_{ti}-gene(s). This may have resulted in a non-identification of very weak Ne-alleles, like the $Ne_1{}^w$-allele of Chinese Spring, in dry years in the field. In the green-house sufficient water prevented withering before the first symptoms appeared.

The tester lines were checked for presence of the relevant Ne-allele. This was done by crossing the tester lines with varieties possessing the complementary Ne-allele.

3. *MATERIAL*

Seeds of the tested varieties were obtained from various genebanks and other collections (see for sources: ZEVEN, 1965-1976). The main sources were the Plant Genetics and Germplasm Institute, Beltsville, Maryland, USA, the Vavilov Institute of Plant Industry, Leningrad, USSR and the Zentral-Institut für Genetik und Kulturpflanzenforschung, Gatersleben, DDR. The origin of the material was checked to avoid inclusion of improved varieties with exotic genes. Only line selections from local varieties were included. See for the origin of most of the material ZEVEN & ZEVEN-HISSINK (1976). Published information was studied and many personal inquiries were made to establish the correct background. If errors occur, it is believed that these are few and of negligible influence.

As most of the material consisted of recently collected samples of local varieties, these samples were often morphologically impure, and in some cases, also for Ne-genotype. However, never was a variety found that was both an Ne_1- and an Ne_2- carrier.

In all, 1100 local varieties of bread wheat and line selections of such varieties have been studied. Their number per nationality is given in Table I. The present nomenclature of *Triticum/Aegilops* is rather complicated. In this paper I will use the «specific» names only when necessary, as it reduces the space taken up by lengthy scientific names. So instead of writing *Triticum turgidum* ssp. *turgidum* conv. *durum* I will write durum, or durum wheat. I also will use the name *Aegilopa squarrosa* instead of *T. tauschii*.

Modern European and US varieties have been identified as Ne_1-, Ne_2- and non-carriers. Their breeders, variety registrars and farmers do not know the Ne-genotype of the variety they bred, registered or cultivated. Apparently there is no advantage or disadvantage for a variety in possessing an Ne-allele. This shows that the Ne-alleles are neutral and that the old bread wheat varieties spread irrespective of the presence of an Ne-allele.

Archaelogical finds show that wheat were grown as mixtures. Such mixtures occured recently in the Austrian Alps where vulgare and compactum wheats were grown together (MAYR, 1964). They are presently grown in Afghanistan (HALLORAN, 1966; DOROFEEV, 1969; BENNETT, 1970) and in Anatolia

Table 1. — Numbers of varieties tested and classified according to their Ne-genotype (1)

Country	Ne_1^m	Ne_1^w	Ne_2^s	$ne_1 ne_2$	Total
Afghanistan	2			6	8
China + Taiwan	4	6		10	20
Cyprus				1	1
India	4	12		17	33
Iraq				1	1
Iran	1	2		5	8
Israel	1			6	7
Korea	1	2			3
Mongolia				1	1
Nepal	1			10	11
Pakistan	4	11		24	39
Philippines				2	2
Saudi-Arabia + Yemen	13	2		12	27
Tibet	1	2		2	5
Turkey	10			2	12
Asia (except Asian USSR)	**42**	**37**	**0**	**99**	**178**
Algeria	3			7	10
Canary Islands	1	3		14	18
Chad	4			2	6
Egypt	9	1		5	15
Ethiopia	1	2		4	7
Lybia	19			9	28
Morocco	4	3		66	73
Nigeria	45			18	63
Sahara	1			7	8
Soudan	1	1		2	4
Tunisia	4			22	26
Africa	**92**	**10**	**0**	**156**	**256**
Albania		1	1	3	5
Austria			10	70	80
Belgium			1	1	2
Bulgaria			1	1	2
Czechoslovakia				4	4
Denmark			1	2	3
Finland			10	9	19
France	4	1	17	38	60
Germany**	1		6	40	47
Great Britain	3	3	12	23	41
Greece			4	17	21
Hungary			18	111	129
Ireland				5	5
Italy	5	6		23	34
Malta				1	1
Netherlands			1	7	8
Norway				6	6
Poland			4	7	11
Portugal	1	8		20	29
Rumania	1				1
Spain		3	1	14	18
Sweden			3	14	17
Switzerland	1		2	12	15
USSR	35	7	22	65	129
Yugoslavia		1		6	7
Europe (incl. USSR)	**51**	**30**	**114**	**499**	**694**
Total	**185**	**77**	**114**	**754**	**1130**

(1) Ne_1^m: $Ne_1^m Ne_1^m ne_2 ne_2$; Ne_1^w: $Ne_1^w Ne_1^w ne_2 ne_2$; Ne_2^s: $ne_1 ne_1 Ne_2^s Ne_2^s$; $ne_1 ne_2$: $ne_1 ne_1 ne_2 ne_2$. — * Incl. Ne_2^{ms}; ** FGR and DDR.

and Transcaucasia (DOROFEEV, 1968, 1969). Such mixtures are likely to have received a vernacular name, which often means wheat *in sensu lato*, cereal or corn.

4. LITERATURE AND PERSONAL COMMUNICATIONS

Many data were derived from literature and obtained by personal communications. The sources have been listed by ZEVEN (1965-1976).

5. THE OBJECT OF RESEARCH

The object of research is to determine the geographical distribution of Ne-genes and their alleles in indigenous «local varieties», and to use the data for investigation of the spreading of bread wheat over the Old World.

As will be discussed later, bread wheat reached Europe, Africa and possibly SW Asia as an admixture of emmer. The routes by which emmer spread are documented by archaeological investigations. Bread wheat spread to East Asia unaccompanied by other cereals.

It could be argued that the recent distribution of local varieties of bread wheat has no or little relation with the original spreading pattern as the latter could have been disturbed by secondary imports of bread wheat. However, there are are only a few reports on the transport of wheat. Thus in Ancient Rome wheat was imported from North Africa and from East Mediterranean areas (CAESAR, 44 B.C.; MANN, 1946), but the imported wheat was mainly durum wheat (KAYYEL, 1973). Bread wheat came from Gallia and elsewhere. Much later the import of wheat into industrializing Europe developed; maybe the first war between wheat merchants of North Sea and Baltic parts took place in 1280 A.D. (PORTHEINE, 1898). Still later, larger imports into NW Europe arrived by the so-called Horseshoe Trade from N. Poland and SW Russia and their interlands. But these wheats were not introduced as sowing seed and we do not know how much reached the farms. The fast spread of an Ne-allele came by the introduction of Ne_2^m-carrying Mexican short straw bread wheats as sowing seed and breeding material. This fast spread was made possible by modern means of transport and extension work, two factors which only arose in recent time.

So we do not know the genetic impact of secondary introduced wheats on the original populations, but as literature rarely refers to transport of wheat and as we do find geographical patterns for the Ne-alleles it is assumed that this impact, except for the introduction of Ne_2-carriers into NW Europe (see below), was quite limited or absent up to ca. 1900. So identically to the geographical patterns of the human blood group loci and alleles after the immigration of the first farmers into Europe. These patterns still show that these farmers came from SE Europe migrating in NW direction (DARLINGTON, 1969; ME-

NOZZI et al., 1978). The movement of man and wheat was very limited.

The spread of agriculture and wheats into Europe, West and SW Asia, and Africa happened in an area that was free of agriculture and consequently free of wheats. But in eastern direction, the more east the wheats went, the more numerous the other domesticated crops they met, like rice, etc. This may have slowed down the spreading of the migrating wheats. Thus HO (1962) reported that wheat reached North China in 1200 B.C., while it reached Japan only in 300 B. C. (KIHARA, 1969).

A more precise description of the routes of spread, when available, will be given when discussing below the various regions.

6. RESULTS

6.1. GEOGRAPHICAL DISTRIBUTION OF NE-ALLELES

In earlier publications I proposed a division of the Old World into areas where certain alleles of Ne_1 or Ne_2 dominated. On account of new results and after consideration of all data I have partly abandoned the old division of non-carrier areas. Below I will show that the non-carrier areas are linked to form one extremely large non-carrier area. However, for the sake of convenience in discussion and after some adaptations I will use the original division of non-carriers (map 1) :

Non-carrier area 1 : Ireland - Great Britain - France - Belgium - the Netherlands - Germany - Denmark - Norway - Sweden - Poland - Czechoslovakia - Bulgaria - Hungary - Yugoslavia - Albania - Austria - Switzerland.
non carrier area 1 links with :

Non-carrier area 2 : Canary Islands - North Africa - Sahara - Israel - Syria - Libanon - the Mediterranean Isles - South Greece - South and Central Italy - Spain - Portugal.
non carrier area 2 links with area 1 and

Non-carrier area 3 : Ethiopia.
non carrier area 3 links with area 2 and

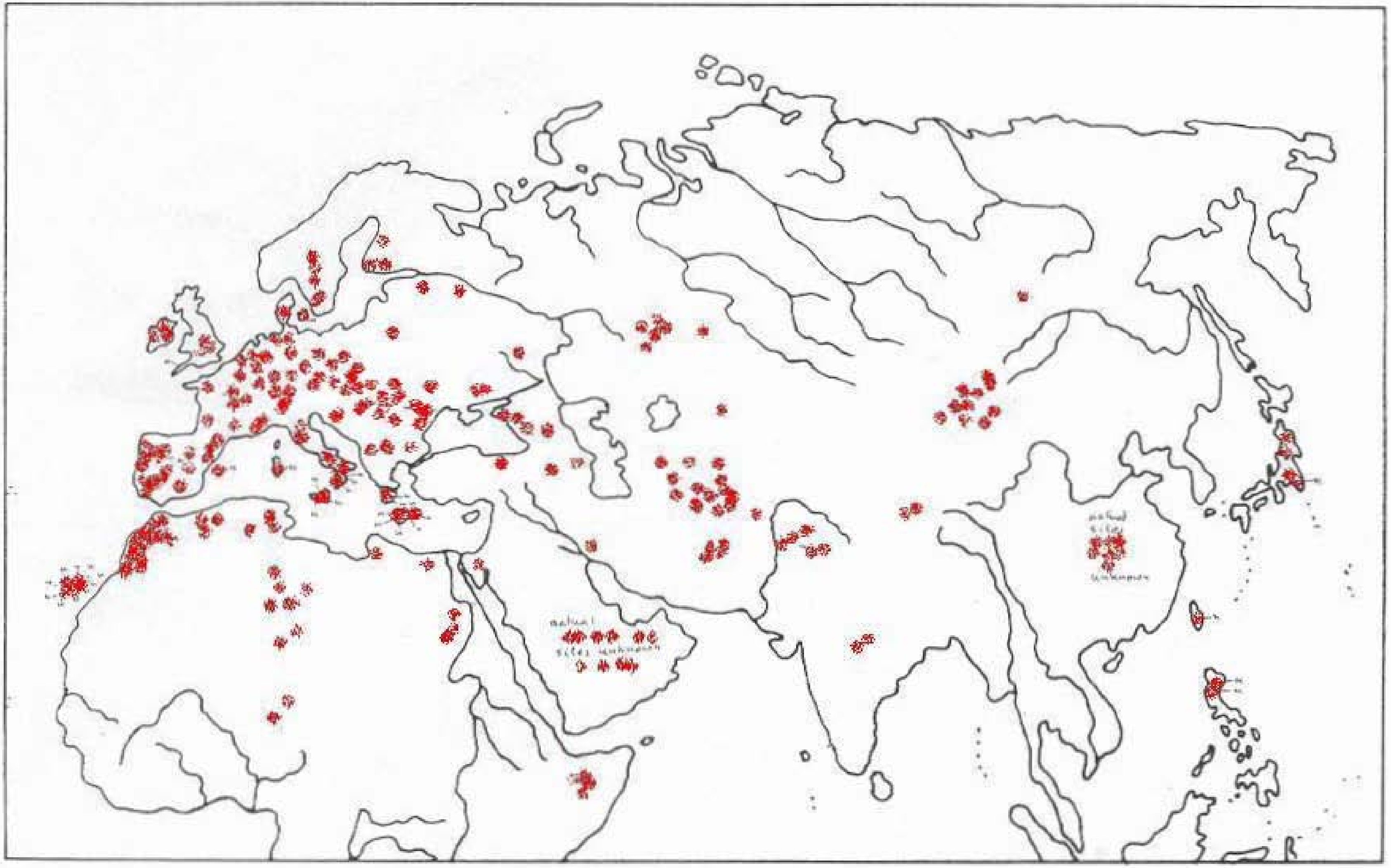
Non-carrier area 4 : Saudi Arabia - Southern Iran - Afghanistan - Uzbekistan - Tadzhikstan - Kirgizstan - Kashmir - up to Lake Baykal and Trans-Baykal regions - Mongolia - Mandchuria - East China - Taiwan - Japan - Philippines.

For Ne_1 and Ne_2 we established the following areas (map 2 and 3) :

Ne_1^w area 1 : northern Portugal - northern Spain - southern France - Italy - Albany - West Greece.

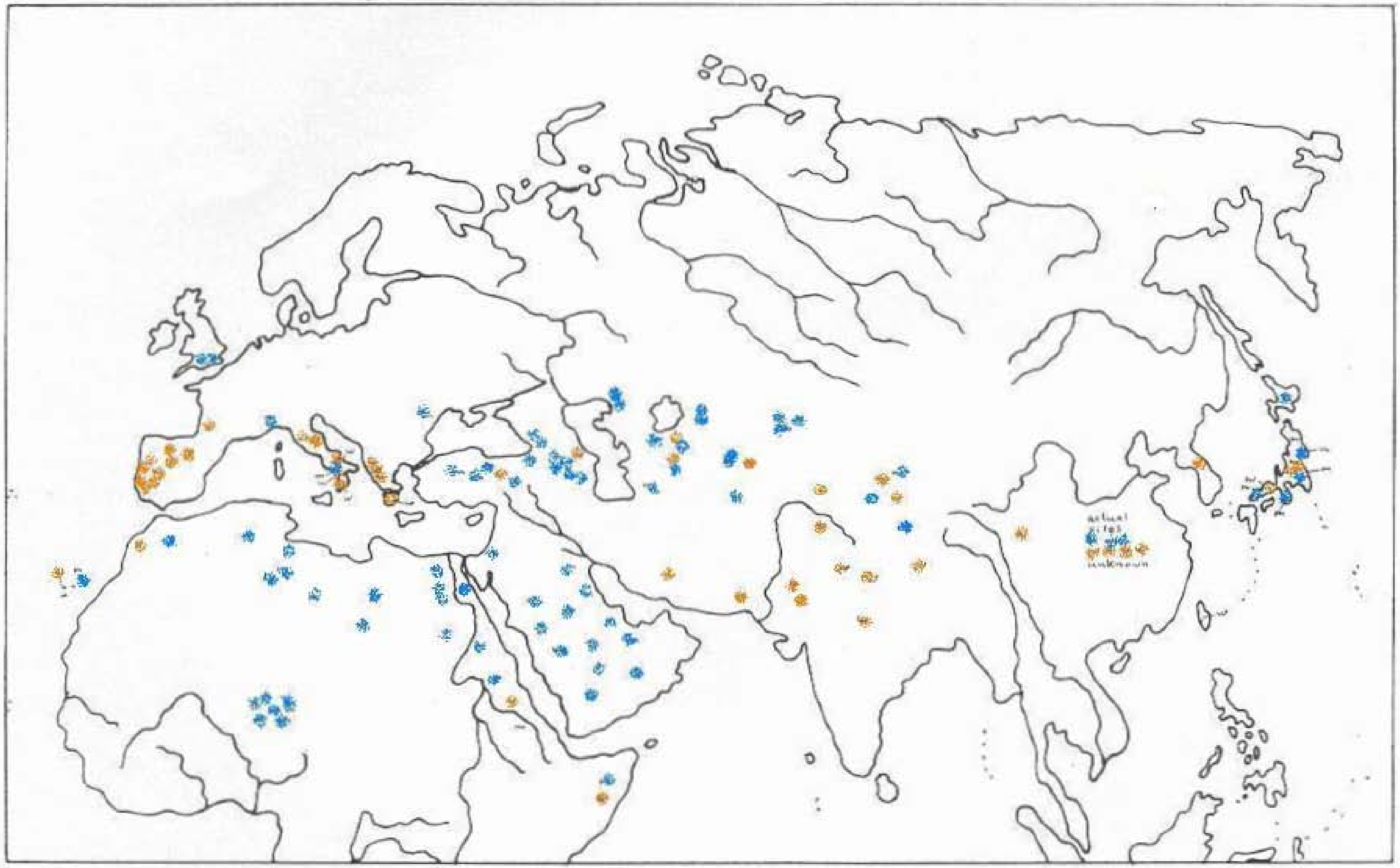
Ne_1^w area 2 : southern Iran - southern Pakistan - India - South China and, most likely, East China.

Ne_1^m area : the Sudan zone - some Sahara oases - the Arabian Peninsula -



Map 1. – The geographical distribution of non-carriers (✲ genotype n_1 ne_1 ne_2 ne_2).

Map. 2. — The geographical distribution of $Ne_1{}^w$ (●; genotype $Ne_1{}^w Ne_1{}^w ne_2 ne_2$) and of the $Ne_1{}^m$ (●; genotype $Ne_1{}^m Ne_1{}^m ne_2 ne_2$).



Turkey - Iraq - northern Iran - Transcaucasia - Turkestan - Kazakhstan - upto North and East China - Japan.

$Ne_2^{ms/s}$ area 1 : White Russia - Bulgaria - Poland - Finland.

$Ne_2^{ms/s}$ area 2 : Switzerland - France - Belgium - the Netherlands - upto Sweden.

No Ne_1^s area has been found for bread wheat. This accords with the fact that this allele belongs to naked tetraploid wheats like durum and carthlicum wheats.

Land varieties with Ne_2^m, Ne_2^{mw} and Ne_2^w occur rarely and no geographical distribution for these alleles could be found.

6.2. ON THE ORIGIN OF EMMER

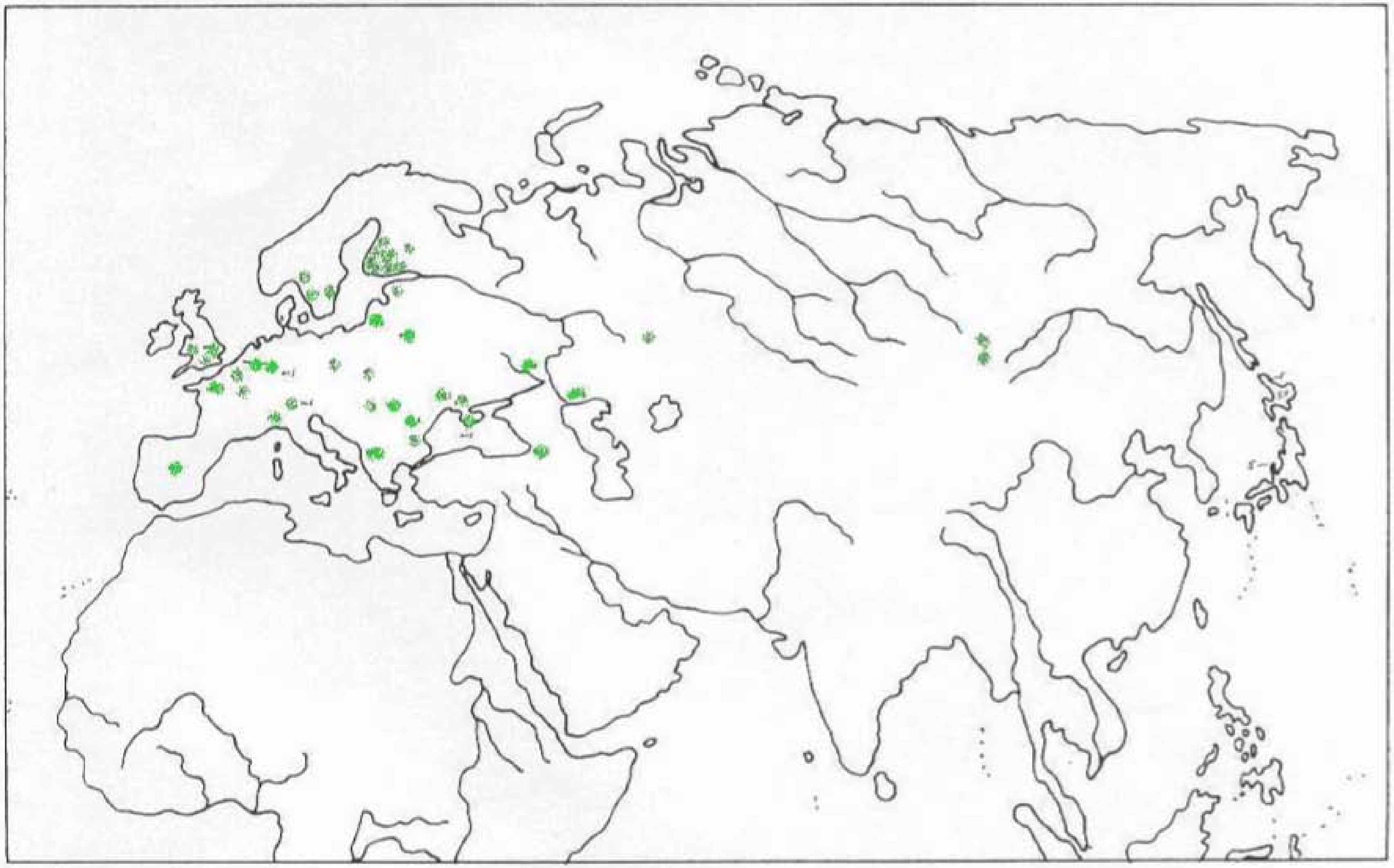
It is generally assumed that emmer is the domesticated type of wild emmer *(dicoccoides)* (see ZEVEN & ZHUKOVSKY, 1975). However, DENNELL (1973) said that: «present evidence suggests that by 7000 B.C. a tough-rachis tetraploid wheat was cultivated in various areas of the Near East. Shortly after this date the first record of *T. dicoccoides* is found (Jarmo and Cayönü)». So *dicoccoides* would have originated later as a feral offshoot of *dicoccum*. Or *dicoccoides* would have originated as a new amphidiploid of *boeoticum* + *Aegilops speltoides* DENNELL, 1973). However, VAN ZEIST (1976) stated that *dicoccoides* also occured in the earliest remains of emmer. So, unless new evidence becomes available, the above assumption - emmer (dicoccum) is the domesticated derivative of the wild emmer *(dicoccoides)* - should be maintained.

6.3. DOMESTICATION OF EINKORN AND EMMER AND ON THE ORIGIN OF BREAD WHEAT.

DHALIWAL (1977) concluded that einkorn *(monococcum)* is quite uniform. And as its parental species *T. boeoticum* is heterogeneous, only a small population of wild einkorn has been domesticated to become einkorn. So einkorn would have developed into a domesticated crop in a restricted area within a short period after it had been moved from the area of wild einkorn.

The conclusion that einkorn is quite uniform is correct, but I will come to it by a different way. The first population of a somewhat domesticated einkorn existed of a number of genotypes that represented more or less the genetic variation of its wild (starter) population. Due to intergenotypic competition only a limited number of genotypes survived. This genetically poor einkorn population served as a nucleus population from which all other einkorn populations derive. The first populations of domesticated einkorn must have been taken quickly outside the area of the wild einkorn. Otherwise the genetic variation of einkorn would have increased due to introgression of wild einkorn genes.

Map. 3. – The geographical distribution of Ne_2^{ms} (; genotype $ne_1\,ne_1\,Ne_2^{ms}Ne_2^{ms}$) and Ne_2^{s}-carriers (genotype $ne_1\,ne_1\,Ne_2^{s}Ne_2^{s}$).



Similarly, the «European» emmer is genetical poor in Ne-alleles and carries only ne_1 and ne_2 while the wild emmer carries several Ne_1-alleles and ne_2. This may also point to a domestication of a small wild emmer population, intergenotype competition and a quick transportation away from the wild emmer area.

The origin of bread wheat is discussed below. It is not known whether bread wheat has a monophyletic or a polyphyletic origin. If a monophyletic origin is advocated the first hexaploid wheat must have had the Ne-genotype of the parental emmer plant. If a polyphyletic origin is supported, more Ne-genotypes of emmer would have been parents to bread wheat. We know that in bread wheat various Ne-genotypes occur, but we do not know whether these different Ne-bread wheats originated from several (emmer + *Ae. squarrosa*) amphiploids different for the Ne-genotype or whether the Ne-alleles introgressed at a later date.

«European» bread wheat was spread together with «European» emmer, both being non-carriers (Table 2 for emmer). But not all emmer wheats are related to bread wheat (and to «European» emmer). So the «Indian» emmer - khapli - carriers Ch_1 (HERMSEN, 1966). This allele is not found in bread wheats *(vulgare, compactum, sphaerococcum)*. It must be related to the hexaploid makha *(macha)* wheat, which also carries Ch_1. Whether the non-carrier bread wheat arose and spread first followed by Ne_1- and Ne_2- carriers is not known. From the geographical distribution of these wheats in Europe, Africa and SW Asia no conclusion can be drawn. Maybe when the geographical distribution of the Ne-genotypes in China becomes available more can be said about it.

Table 2. – The genotype for hybrid necrosis, hybrid chlorosis and fertility restoration of timopheevi cytoplasmic male sterility.

Variety	Nationality	Genotype
Weisser Emmer	Austria	$ne_1 ne_2 ch_1$ (rf)*
Wörther Emmer	Austria	$ne_1 ne_2 ch_1$ (rf)
Amedonier noire	France	$ne_1 ne_2 ch_1$ (Rf)
Weisser Amedonier	France	$ne_1 ne_2 ch_1$ (rf)
Baj. Begrannter (1)	Germany	$ne_1 ne_2 ch_1$ (rf)
Eichenberlebener	Germany	$ne_1 ne_2 ch_1$ (rf)
Graüer Emmer	Germany	$ne_1 ne_2 ch_1$ (rf)
Roter K. Halbbegr. S. (2)	Germany	$ne_1 ne_2 ch_1$ (Rf)
Asturische Emmer	Spain (Asturia)	$ne_1 ne_2 ch_1$ (rf)
Balkan 1941 : 2588	Yugoslavia	$ne_1 ne_2 ch_1$ (rf)

(1) Bajonetförmige Begrannter. (2) Roter Kahler Halbbegrannter Sommer. * (rf) : no. of genes not determined.

6.4. *ARE THE NEOLITHIC AESTIVO-COMPACTUM GRAINS POSSIBLY GRAINS OF DURUM WHEAT?*

Many authors have identified wheat grains of archaeological findings with a plump character as grains of bread wheat. On the basis of their plumpness they were classified as *«aestivo-compactum»*. Such plump grains already occured in grain mixtures of 6000 B.C. So it was concluded that bread wheat existed already at that time.

Since bread wheat arose from a cross between emmer and the wild grass *Aegilops squarrosa* followed by amphidiploidisation, this could only have happened after the origination of emmer and its transport to the area where *Ae. squarrosa* occurs in a wild state. This would have been the case in the period 6000-5000 B.C. (VAN ZEIST & BAKKER-HEERES, 1975, VAN ZEIST, 1976). These researchers concluded that the grains hitherto identified as «aestivo-compactum» can therefore not be bread wheat grains. Seing that durum wheat grains resemble those of bread wheat so closely that they cannot be told apart, the *«aestivo-compactum»* grains are considered to be in fact durum grains. This conclusion was supported by the evidence that, if the first hexaploid wheat is an amphidiploid of emmer (brittle rachis, genotype qq) and *Ae. squarrosa*, this wheat would have carried a brittle rachis too. The first hexaploid wheat would then have been a spelt-like wheat. However, spelt grains in archaeologic finds date later than the *«aestivo-compactum»* grains. The occurence of durum wheat in the Neolithicum would fit in better with the theory of evolution, i. e. the tough-rachis durum (genotype QQ) could easily result from a mutation (q ——> Q) within emmer. At a later date durum could have reached *Ae. suqarrosa* after which the tough-rachis bread wheat arose.

Arguments against the conclusion of *«aestivo-compactum»* grains being durum grains are :

1. Tough-rachis wild emmers have been found though it might be argued that they arose from an introgression of the Q gene into this wild species.

2. Present day durum wheats are mainly $Ne_1{}^s$-carriers (SARKISIAN et al., 1971; ZEVEN, 1976) and, if emmer and durum wheats would have been grown as a mixture the $Ne_1{}^s$-gene would certainly have introgressed into the European emmer. I have no evidence that the latter species carries $Ne_1{}^s$. A counter-argument could be that the first durum wheats, like their parental emmer, were non-carriers, and that they differ in this respect from the present day durum. However, VAN ZEIST c. s. also based their conclusion on the close resemblance of present day bread wheat grains and those of present day $Ne_1{}^s$-carrying durum wheats.

3. It is not known whether the present day distribution of *Ae. squarrosa* is the same as its spread some 9000 years ago. This argument was also advanced by VAN ZEIST c. s. It could be assumed that a few caryopses of *Ae. squarrosa* had reached a field of emmer.

4. The small number of finds dating about 6000 B.C. and the few data available are not sufficient to prove that farming + emmer reached *Ae. squarrosa* only after «*aestivo-compactum*» had arisen.

6.5. THE SPREAD OF BREAD WHEAT OVER THE OLD WORLD

To make a discussion more convenient, we still separate the Old World into parts which are based on the «streams» or routes by which bread wheat was spread over the Old World.

6.5.1. Centre of origin and diversity of bread wheat

In Caucasia bread wheat varieties carry Ne_1 or Ne_2 or are non-carriers (DOROFEEV & MEREZKO, 1969; MEREZKO, 1970; DEKAPRELEVICH & YASHAGASHWILI, 1970; DEKAPRELEVICH & NASKIDASHVILI, 1971; SARKISIAN & PETROSIAN, 1972; MKRCHIAN & MINASSIAN, 1973; ZEVEN, 1973; TSUNEWAKI & NAKAI, 1974). This could mean that Ne_1 and Ne_2 are indigenous there. However, on the opposite side of the Black Sea we find in Crimea and the Ukraine Ne_2-carriers. It is quite possible that wheats from these regions were introduced into Caucasia. Similarly we find an Ne_1m-carrier (Ulka) in Rumania, which must have been introduced from Turkey or Caucasia. Further research of genotypes should be done to solve this problem.

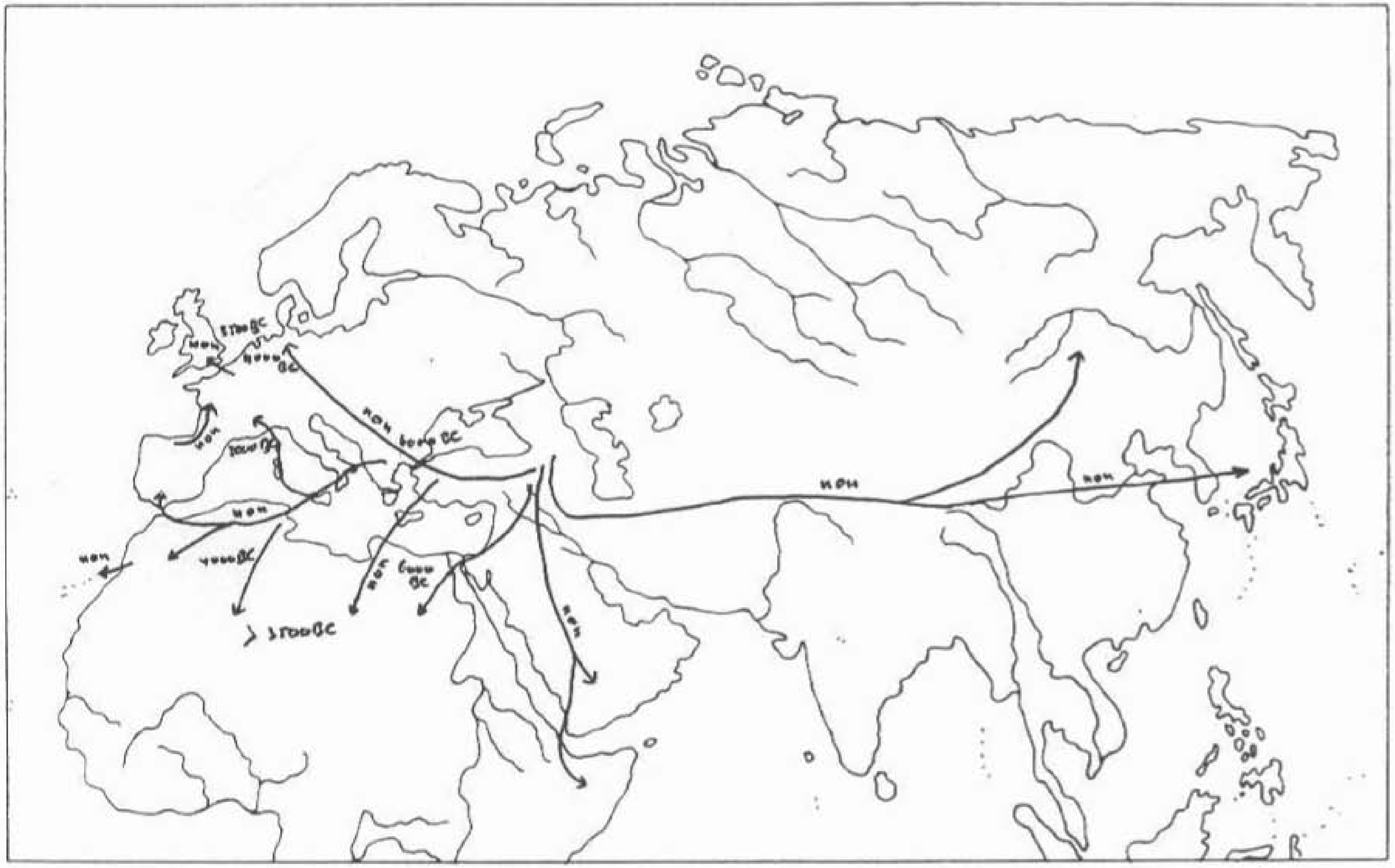
6.5.2. Europe except USSR and the Mediterranean Basin.

This region and others include the non-carrier area 1 and the Ne_2ms/s area 2.

HOPF (1975) described the main routes (map 4) by which agriculture and the wheats reached Europe and Africa. One route started in the Near East to cross the Bosphorus into Greece soon after 6000 B.C. (RENFREW, 1973). This route branched in Bulgaria with one branch going northwards to reach Moldavia. However, RENFREW (1973) stated that the wheats could have reached Bulgaria direct from Turkey. The second branch goes northwest with the Danubian Aryan farmers (Band Keramic Culture) through the Balkans northwards into Poland, Denmark and Sweden: Some examples are: emmer and bread wheat occured in the Balkans in ca 6000 B.C. (RENFREW, 1973). These wheats got to the loess plains of Central Europe in ca 5000 B.C., and reached Belgium and the south of the Netherlands in ca 4000 B.C. (BOHMERS, 1958/1959; DE PUYDT et al., 1910). In the fourth millenium agriculture and wheats gradually entered other parts of North and West Europe (CLARK, 1956).

So agriculture and wheats moved into Europe with a mean speed of some 1km/year. SPANG et al. (1976) showed that agriculture was introduced into the whole of Denmark by 4200 B.C. At that time it had also reached the south west area of Sweden after its introduction from Denmark. From there it moved north west, north and northeast into Norway, Central Sweden and Finland.

Map. 4. — The routes of spread of non-carriers and period of the first introduction.



By 2800 B.C. most of south-west Finland was acquainted with farming and hence with wheats.

Another main route, also starting in the Near East crossed the Dardanelles to branch in Greece, one branch going south, the other north-west as far as the north of Italy and West and North-west Europe. WATERBOLK (1971) and BUTZER (1971) summarize the areas where farming had been introduced at various epochs.

Farming had reached many places in Europe by 5000 B.C. Within ca 800 years from then farming and wheats had covered most of Europe. The production areas were also the consumption areas; long distance transport could only become a fact when transport over water developed. This means that wheats did not move over a large distance after they had reached a certain site (JARMAN & BAY-PETERSON, 1976). These authors also mentioned that the neolithic wheat production areas in Europe are still the present day production areas of the crop.

Most of the finds show us that wheats were grown as mixtures in which emmer was the main crop, but occasionnally with bread wheat was the dominating component. For instance VAN ZEIST & BAKKER-HEERES (1974) found on a farmer's site in East Central Turkey dating 4500-4000 B.C. 40 (75%) emmer grains and 9 (15%) bread wheat grains. For a find of 4200 B.C. they discovered 62 (82%) emmer grains and 14 (18%) bread wheat grains. At that time and upto ca 2300 B.C. no einkorn was grown there; elsewhere it was. In the period 2600-2300 B.C. emmer had almost disappeared and bread wheat had become the main wheat crop.

Other examples are from Bulgaria (HOPF, 1973) :

period	number of grains and percentage			
	einkorn	emmer	bread wheat	n
4900 B.C.	9 (4.0%)	218 (96.0%)	0	227
4800 B.C.	3	ca 6		ca 9
4770 B.C.	22 (2.9%)	204 (27.1%)	527 (70.0%)	753
4275 B.C.	- (0.0%)	- (99.0%)	- (0.0%)	-

So two samples are almost pure emmer, but in the sample of 4770 B.C. bread wheat makes out 70% of the grains. More examples are presented by HOPF (1968).

There must have been special, but unknown conditions which made bread wheat or einkorn become the main crop instead of emmer already at an early time. For instance, einkorn was the principal wheat at a site in N. Yugoslavia. There the first bread wheat-like grains were identified dating from 3000 B.C., while bread wheat as a mixture of emmer and einkorn was grown there ca 2500 B.C. VAN ZEIST & CASPARIE (1974) found only bread wheat grains ar Niederwil, Switzerland, dating from ca 3700-ca 3625 B.C.

In a Neolithic site (Vlaardingen, the Netherlands, dated 2350 B.C.) 69 (90.8%) bread wheat grains and 7 emmer grains were discovered. At other sites of the Vlaardingen culture emmer was the sole crop. At Roman site bread wheat was the main crop (VAN ZEIST, 1968). This proofs that in the Neolithic bread wheat as such was an important crop. The more or less pure wheat populations must have originated from a demixing of the introduced emmer/bread wheat/ einkorn mixtures. But why were they demixed?

6.5.2.1. THE ALPINE WHEATS.

In the valleys of the Austrian (and Swiss) Alps Alpine bread wheats have been grown up to recent times. They are extremely old and are direct descendants from the wheats cultivated by the Palustrian farmers at ca 4000 B.C. (MAYR, 1964; KOCK, 1973; SCHACHL, 1975a, 1975b), which have also been described by O. Heer as *Triticum antiquorum*. The local varieties were mixtures of vulgare and compactum. In the higher valleys only spring wheats could be grown. In the lower valleys both winter and spring wheats occured. KOCK (1973) stated that the spring wheats of the higher valleys had been introduced earlier than those of the lower valleys. In the isolated valleys the spring wheats were completely adapted to the local climatic conditions. KOCK suggested that no other wheats could be introduced, as they were not suitable for these places. I doubt whether this picture is as black and white, as suggested. Some gene exchange may have occured and its impact over several millennia must have been enormous.

The Palustrian alpine wheats must derive from the bread wheat admixtures of emmer. Apparently owing to natural and/or human selection, the emmer wheats must have been suppressed. So their original genotypes should be equal to those of these admixtures, hence to very early bread wheat. But the extent of introgression is not known. By investigating the genotypes of a number of recently collected Alpine wheats we may get an indication of their original genotypes. If so, these original genotypes can be compared with those of the European emmers. The latter are direct descendants from the emmers imported and cultivated by the Danubian farmers. An indication of relationship is that the present day land races of emmer and bread wheat of Europe are non-carriers. Fifty-five bread wheats of Austria have been tested; the 21 spring wheats are all non-carriers, the 34 winter wheats divide into 26 non-carriers and 8 $Ne_2^{ms/s}$-carriers. This Ne_2-allele, which is also found in some Swiss bread wheats must originate from later introductions and/or from introgression with spelt. Spelt is mainly an Ne_2-carrier (ZEVEN, 1969, 1971a, 1971b). As the Alpine wheats do not carry this allele, spelt cannot derive from a cross between Alpine wheat x emmer.

6.5.2.2. POLAND AS AN EXPORT COUNTRY.

Poland is also included in non-carrier area 1, although many varieties carry an Ne_2-gene. During the last 4-5 centuries much mixing must have occured there. Poland exported a great deal of wheat from ports as Szczecin (Stettin) and Gdansk (Danzig) and these arrived there via the rivers Neisse and Wisla (Weichsel) (KOSTECKI & WOLSKI, 1963). Elsewhere such wheats were sown and grown to develop into local varieties. The names of some Irish varieties like Red Stettin or Danzig refer to their origin, but this is not the case for Irish Red Chaff, which is a synonym of Red Stettin. Nor does Red Fife give an indication of its Polish origin. It developed in Scotland from Ostka Galicyjska, which means bearded (wheat) from Galicia, South Poland. The origin of these introductions is traceable; but how numerous are those that cannot be traced? Hence it is concluded that the Ne_2-local wheats of West Europe derive from imports from East Europe, creating a second Ne2-area in a non-carrier area.

The shipment of wheat and other transports within Poland must have caused the Ne_2-carriers and non-carriers to mix there. The Irish wheats Red Stettin and Danzig are non-carriers. Maybe they derive from non-carrier wheats of Poland. Red Fife is an Ne_2^s-carrier and thus belongs to the wheats of Ne_2^s-area 1. Other non-carriers can have reached West Europe, but they merely shifted from the east end to the west end of non-carrier area 1.

Another, more recent influx of Ne_2-wheats into non-carrier area 1 happened in Hungary, where in 1863 the wheat harvest failed and sowing seed (of local varieties) had to be introduced from Galicia and West Ukraine (JANOSSY et al., 1963). The Ne_2-wheats may derive from this and similar imports.

6.5.2.3. GREAT BRITAIN AND IRELAND

HOPF (1975) stated that agriculture reached Great Britain and Ireland from Central Europe, whereas RENFREW (1973) wrote that it was introduced via the Mediterranean - Spain - Atlantic coast route. Maybe both routes were used. Our data are of no help in determining the correct route. Both areas belong to the large non-carrier area and hence the first bread wheats came either from Central Europe or from North Spain. West France is a non-carrier area. We have tested 38 local varieties from Great Britain and 4 from Ireland which were grown around 1900. The results are :

Ne-genotype	GB		IRL	
	No	%	No	%
Ne_1^m	1	2.6	0	-
Ne_1^w	2	5.3	0	-
$Ne_2^{ms/s}$	13	34.2	0	-
Non	22	57.9	4	(100)

The three Ne_1-carriers are of no importance, while the Ne_2-carriers been introduced from Ne_2-area 1 (see above). Among the 22 non-carriers several probably derive from non-carrier varieties introduced in the last few centuries. The remainder may originate from the introduced ca 5000 B.C. non-carrier wheats. Three of the four non-carrier wheats from Ireland are known to come from Poland, while the fourth is called Galway landwheat. It may or may not have been introduced in the last centuries.

Further research should be done to determine which of the land wheats belong to the earliest introduced wheats and from where they came.

6.5.2.4. SOUTH FINLAND.

Agriculture and non-carrier wheats reached south-west Finland 2800 B.C. (see 6.5.2.), but agriculture did not continue and the wheats must have died out. Apparently, Finland was populated by immigrating farmers who came from the south crossing the Gulf of Finland (NEVANLINNA, 1972). This immigration came to a halt around 800 AD. The origin of the Finnic people from which the Finns derive, is not fully understood. But as the Finns grow $Ne_2^{ms/s}$- and non-carriers the Finnics must have come from or by way of the $Ne_2^{ms/s}$ area 1 (map 5) (see 6.5.2.5.). They may have also transported non-carrier wheats taken from the European or Asian non-carrier area. For instance, PISAREV (1956, 1960) stated that bread wheats were taken from the Trans-Baykal into Siberia and hence into Finland. If so the non-carrier wheats of Finland could also (partly) derive from the non-carriers of Trans-Baykal. This needs further investigation.

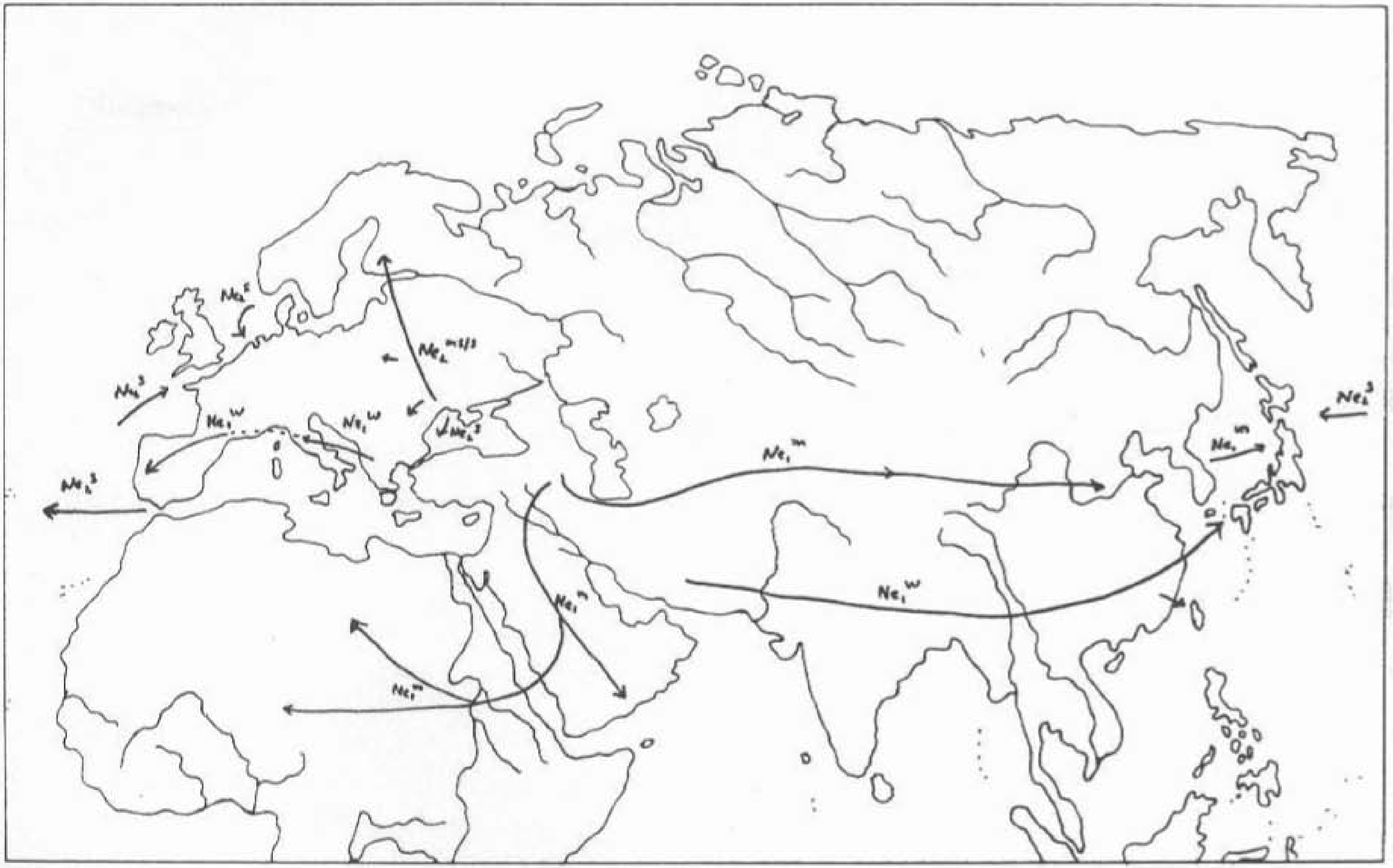
6.5.2.5. $Ne_2^{ms/s}$ AREA IN EASTERN EUROPE

In area 1 in the $Ne_2^{ms/s}$ allele must have originated either as a mutation or through introgression. In the latter case the source is unknown. *Aegilops speltoides* played perhaps a role, because F_1 plants (durum Ne_1^s x *Ae. speltoides*) showed symptoms of modest hybrid necrosis (ZEVEN, 1971). This means that this accession of *Ae. speltoides* carried Ne_2. Furthermore, the Ne_2/ne_2 locus is located on the 2 B chromosome (TSUNEWAKI, 1960) which probably derives from this *Aegilops* species.

From the nucleus «Crimea-Ukraine» $Ne_2^{ms/s}$ wheats were taken northwards (map 5) to mingle with non-carriers in South Poland, South Finland and other regions. Area 1 may have been the area of origin of the Ne_2-wheats of Ne_2 area 2 (see below). The $Ne_2^{ms/s}$- allele also spread in western direction into the Balkan, while the few Ne_2 wheats of Switzerland possibly also derive from imports. However, there is also possibility that this allele introgressed from *spelta*. This wheat was cultivated in South Germany, Switzerland and elsewhere. Spelt wheat and the non-carrying bread wheats cannot be closely related as *spelta* carries Ne_2^s (see 6.5.2.1.). Area 1 is thought to be also the source of the so-called Mediterranean and Turkey wheats grown in North America.

In quite recent times Ne_2^s bread wheats were taken by Russian colonists to the region around Irkutsk (ANON., 1949; BAHTEEV, 1960).

It is tempting to relate the $Ne_2^{ms/s}$ nucleus with the neolothic farmers of the Tripolie culture (ca 3500-1900? B.C.). They grew wheat and other crops (JANUSHEVICH, 1978).



Map. 5. — The routes of spread of $Ne_1{}^{m}$-, $Ne_1{}^{w}$- and $Ne_2{}^{s}$-carriers.

6.5.2.6. $Ne_2^{ms/s}$ AREA 2

It has already been suggested (see 6.5.5.2) that the Ne_2 wheats of West and Northwest Europe derive from import wheats from Ne_2-area 1. These wheats had arrived in West and Northwest Europe mainly by the Horseshoe trade in the last few centuries (map 5).

6.5.3. The Mediterranean basin

6.5.3.1. NON-CARRIER AREA 2.

HOPF (1975) described the spread of emmer wheat through the Mediterranean (map 4). From the Near East a stream of emmer went to Egypt. Another stream went to Turkey to divide into one branch going to Lybia and another going to Greece and then to Sicily. Here a further branching occurs. One route goes through Tunisia, Algeria and Morocco to the South of Spain, the second runs through Sardinia to Northeast Spain and then in a southernly direction along the coast. The third route finds France. So agriculture has reached North Africa at several points from the north (HELBAEK, 1960).

According to RENFREW (1973) agriculture was spread by a second route viz. along the Mediterranean coast to Spain and hence along the Atlantic coast to reach the British Isles before 3500 B.C.

If bread wheat was spread together with its parental emmer, it must have been a non-carrier too. There are some finds of bread wheat grains in ancient remains of emmer grains. HELBAEK (1956) discovered in prehistoric emmer from Egypt some *compactum* grains. TELLEZ & CIFERRI (1954) stated that bread wheat was introduced into Spain in the Bronze Age long after emmer had been introduced. But in plant remains from the Spanish East Coast - dating ca 2345 B.C. - HOPF (1971) identified 46 emmer (86.8%) and 7 (13.2%) bread wheat grains. She stated that wheats reached Spain probably in the 5th millennium B.C. This may be an indication of an introduction of bread wheat varieties as such, to replace the emmer with bread wheat mixture. However, from what place or region did these pure bread wheat varieties originate? However, HOPF reported that emmer reached Spain in the 8th Century B.C. and later. Similarly ERROUX & COURTIN (1974) reported the occurence of emmer and bread wheat in South East France ca 3000 B.C. Emmer wheat generally dominated. Einkorn was found only once.

Other researchers give additional and sometimes contradicting information. FLAKSBERGER (1926) reported that in 1500 B.C. wheat (species not mentioned) was exported from Cyprus to Egypt. SCHREIBER (1934) stated that in Sicily bread wheat must have been introduced from the Balearic islands. (When?) Bread wheat was especially grown on Corsica. CIFERRI & GIGLIOLO (1940) wrote that wheats of Rhodos resemble those of the Mediterranean and not those of nearby Anatolia. This accords with our finding that Mediterranean wheats are non-carriers and those from Anatolia Ne_1^m-carriers. Similarly, JAKUBZINER (1932) observed that the Mediterranean wheats resemble those of the Near East. This also agrees with our Ne-data. During relatively less dry conditions of the Sahara (6500-2000 B.C., HOBLER & HESTER, 1969) «bridges» of arable land existed between North Africa and the Sudan zone (map 1). Via these bridges North African non-carrier wheats must have migrated southwards to penetrate into an $Ne_1{}^m$- area (see below) (ZEVEN, 1974). Due to the presence of the first arrived $Ne_1{}^m$ wheat the Sahara became only partly a non-carrier area. If we assume the percentage (12.4) of non carrier wheats among the local $Ne_1{}^m$-wheats from North Nigeria to be representative for the original Sahara wheats, we can estimate how many of the 9 non-carrier wheats from the Lybian oases belong to the first arrived wheats and how many derive from North African imports. The result is : 2 first arrived and 7 later imported non-carriers.

6.5.3.2. $Ne_1{}^w$-AREA 1

The presence of $Ne_1{}^w$-wheats in a narrow band from Greece to Portugal is quite peculiar and I have no information to explain it. WRIGHT's (1972) conclusion that in Spain bread wheats moved more freely round the western end of the Pyrenees into Navarro than round the eastern end finds no support from the Ne-data.

6.5.4. Africa

North Africa has already been treated in the previous section.

6.5.4.1. SAHARA

Agriculture was well established in Egypt ca 6000 B.C. (HUGOT, 1968) and according to CLARK (1962) wheat and barley spread to the Central Highlands of the Sahara in the 5th millennium B.C. (maps 4 and 5). However, HOBLER & HESTER (1969) (see HESTER, 1968) reported that there was incipient food production in Lybia in ca 5950 B.C. This could mean that agriculture was introduced into Africa at an earlier date than hitherto thought. The spread of agriculture must have taken place in the Wet Period, 6000-3500 B.C. About 3000 B.C. knowledge of cereal growing was distributed throughout the Sahara (SEDDON, 1968). HOBLER & HESTER (1969) suggested that the so-called Saharan Fertile Crescent - a chain of highlands in the Sahara - was used as a route by which plants, animals and men migrated. It linked, in dry periods, the savanna areas at the east end with those at the west end. The east end - the Middle Nile region - was the source of the first Sahara wheats (ERROUX, 1962).

These wheats were adapted to the winter rainfalls, which dominated at that time. After increasing dryness wheat and barley could only be cultivated in the Central Highlands, the oases (CLARK, 1964) and in the Sudan zone. The severe conditions in the oases and isolation may have caused the development of wheats with compactoid ear types described as var. *oasicolum* Ducellier (ERROUX, 1962). Crossing var. *oasicolum* with *vulgare* wheat produces an F_2 with an irregular pattern of ear type segregation (ZEVEN, 1967, unpubl.).

This is possibly caused by translocation (ERROUX, 1962). Both the Sahara wheats and those of the Sudan zone (North Nigeria and Chad) are $Ne_1{}^m$-carriers (ZEVEN, 1974). In experiments at Wageningen both prove to be very susceptible to European races of mildew. This could mean that they have a common parentage and that the present-day morphological differences originated from a separate evolution in two very different environments, after their introduction into Africa.

6.5.4.2. ETHIOPIA

Emmer had reached Ethiopia through Egypt, since the present-day emmer of Ethiopia closely resembles the emmer wheat of Ancient Egypt (HELBAEK, 1960). Like the emmer of Europe, bread wheat may have grown there as an admixture. Similarly, ZOHARY (1970) stated that cereals of the Fertile Crescent were likely to have been introduced into Ethiopia by Hamitic agricultural migrants. However, MURDOCK (1959, 1960) suggested that the wheat entered Ethiopia from the Arabian peninsula. Further, JAKUBZINER (1931) reported that the Ethiopian wheats resemble those of Egypt, Syria and Palestine, but VAVILOV (1940) wrote that the wheats of Ethiopia, Yemẹn and India are «linked in origin».

Our data show the Ethiopian wheats to be non-carriers, and therefore, their Ne-genotype is the same as that of many wheats of the Arabian Peninsula, Egypt, Syria and Palestine.

Wheats of South Iran and India are often $Ne_1{}^w$-carriers, and only a few of such carriers have been found in Ethiopia. They may be indigenous, but they could derive from Italian introductions made ca 1935. The Ne-genotypes of the Ethiopian and Indian wheats do not support VAVILOV's observation.

6.5.5. Asia

From its centre of origin bread wheat moved in southern, southeastern and eastern direction. In southern direction wheat reached the Arabian Peninsula, and in southeastern and eastern direction it spread as far as Central India in the south and Japan and the Philippines in the east.

6.5.5.1. TURKEY

From 6.5.2. we learned that the first farmers of Europe migrated through Turkey growing non-carrier emmer and bread wheat mixtures. The oldest cultivated wheat was an emmer wheat grown in Anatolia ca 6750 B.C. (Aceramic Hacilar). The first bread wheats *(vulgare* and *compactum)* date from ca 6500 B.C. (Can Hasan III - aceramic) (MELLAART, 1975). These wheats were very probably the same as those taken some 500 years later into Europe. Hence they must have been non-carriers. At present most of the bread wheats in Turkey are $Ne_1{}^m$-carriers. This suggests a break between the first farmers with their non-carrier wheats and later immigrants farmers with $Ne_1{}^m$ bread wheats. However, nothing is known about such a break (D. FEREMBACH, Juvisy-sur-Orge, personal communication, 1979). Maybe when once attention of archaeologists have been drawn to this possible break it will be observed.

6.5.5.2. ARABIAN PENINSULA

Twenty-seven bread wheats were tested: 1 Ne_1^s, 13 Ne_1^m(48%), 1 Ne_1^w and 12 non-carriers (44%). The Ne_1^m-and the non-carrier wheats apparently occur at random. This may mean that the Arabian Peninsula belongs to an Ne_1^m-area and to a non-carrier area. It is not possible to decide whether the Ne_1^m-bread wheats or the non-carriers arrived first. It could also be that e. g. Ne_1^m-wheats moved along the Red Sea coast and the non-carriers along the coast of the Arabian Gulf. Some support is found for this supposition. The Ne_1^m-wheats of the Sahara came from the Middle Nile region and it is possible that they had been introduced from the opposite side of the Red Sea. WRIGHT (1973) reported that bread wheat entered Iran from the Arabian Peninsula. In Iran we find non-carriers and Ne_1^w-carriers. Except for one, the last are not found in the Arabian Peninsula and therefore Wright must refer to non-carriers, which at the time of introduction into Iran were not contaminated with Ne_1^m-wheats.

6.5.5.3. SPREAD TO ASIA

In Asia we find Ne_1^m-, Ne_1^w- and non-carriers (maps 1 and 2). In West and South Asia these alleles are still restricted to certain regions, but at the east end they have to some extent become mixed with eachother, as here the routes joined.

In 6.5.5.1. it has already been suggested that in West Asia non-carrier wheats may have come from Iran to move eastwards. North of these non-carriers we find Ne_1^m- carriers (Ne_1^m-area, see below) and south we find Ne_1^w- carriers (Ne_1^w-area 2, see below).

As already mentioned, WRIGHT (1973) reported that bread wheats - accor- to us non-carriers - entered Iran from the Arabian Peninsula. Bread wheats reached West China ca 2400 B.C. (LIU, 1927) and Hopei ca 1200 B.C. (HO, 1969). The distance of ca 3400km as the crow flies, was covered in some 1200 years. So bread wheat migrated with an average speed of 2.8 km per year. This is much faster than its speed in Europe (see 6.5.2), and against the supposition made in 5.

However, upto ca 500 B.C. bread wheat had not made much progress in North China due to its poor adaptability to spring droughts (HO, 1969). About 200 B.C. farmers of the Shensi area were ordered to grow more bread wheat. It appears that in the last century B.C. and the first century A.D. two methods were adopted whereby wheat growing became possible. The first is that during the winter snow was pressed together to prevent it from being blown away. Hence at the beginning of spring, the water content of the soil had been increased. The second is the cultivation of spring wheats. It is not known whether these spring wheats were selected from spring types occuring in the local winter wheats or whether they had been introduced. HO (1969) stated that they had been introduced from Central Asia during the Former Han Empire. The

Ne-genotypes of North-Central Chinese wheats as published by TSUNEWAKI et al. (1972) are summarized according to growth habit and Ne-genotype.:

	Ne_1		Non	
	No.	%	No.	%
winter	42	63	48	53
spring	15	22	30	33
interm.	10	15	12	13

The higher proportion of non-carriers among the spring wheats may point to their Central Asian origin, their ratio Ne_1/non carrier does not differ significantly from that of the winter wheats.

It is not reported when bread wheat reached China's east coast and from what direction(s) the first wheats came (see below). KIHARA (1969) wrote that bread wheat entered Japan in ca 300 B.C. This is quite late. HOSONO (1935) is the first to describe the routes by which wheat was transported. One route is India - Burma - South China (Yunnan). This route is characterized by var. *bengalense*. A second is a northern route: Turkestan - Kansu - Shensi. This trade route is characterized by var. *turcomanicum*. In 1954 HOSONO had obtained more data enabling him to develop his views on migratory routes of wheat. He described 3 routes:

1. Afghanistan - Khybar pass - cross the Punjab plain - skirting Himalaya - upper Burma - crossing Yunnan - Szechwan - the Yangtze Valley. By this route red-grained wheats were transported;
2. Turkestan - Sinkian - skirting Mongolia - N. China. This route became later known as the Silk road because of the silk that was traded in western direction;
3. possibly West India - crossing Pamir or Nepal - Shensi or Szechwan. This route could due to lack of data, not be recognized sufficiently. Other scientists have designed other migratory routes for bread wheats.

NAKAO (1957) wrote that wheat was transported via the so-called Persian arc, which runs from Iran to Himalayas. Here this route branched in a western and eastern route. The first keeps its name Persian arc. The eastern branches again in 1. the Himalayan arc (= Indian arc), which runs via the southern slopes of the Himalayan range, and 2. the Tibetan arc which runs along the northern slopes.

NAKAO (1956) described the wheats of Nepal as very similar to those of South and Central China. Earlier LEIN (1949) divided the wheats, collected by the German Hindukush-, India - (Pakistan) - Nepal - and Tibet- expedition in three groups :

1. The Tibetan wheats,
2. the Indian (incl. Pakistani) wheats and

He concluded that the Tibetan wheats have an old, independent evolution and that they form the western population of the East-Asian wheats.

The Indian-Pakistani wheats have a very old, independent evolution too. They are not closely related to the Central Asian wheats. The Hindukush wheats are the eastern population of these Central Asian wheats. Our data do not permit to conclude which is the Ne-genotype of the Tibetan wheats. But, as LEIN concluded that these wheats have some relationships with wheats of Anatolia, it is suggested that the Tibetan wheats are $Ne_1{}^m$-carriers. This needs further proof. LEIN's Indian-Pakistani wheats are $Ne_1{}^w$-carriers (see 6.5.5.3.2) and his Hindukush wheats are non-carriers.

6.5.5.3.1. Non-carriers

Our data suggest that non-carriers were transported north of the Himalaya (map 5). Maybe, at a later time, $Ne_1{}^m$-wheats travelled along the same routes (map 4) (see for the $Ne_1{}^m$-wheat, 6.5.5.3.3.). South of the Himalaya, $Ne_1{}^w$-wheats were transported eastward, so for instance along HOSONO's (1954) first route (map 5). (See for $Ne_1{}^w$-wheats 6.5.5.3.2.).

TSUNEWAKI et al. (1972) tested 21 wheats from Mandchuria. Two were Ne_2- carriers and therefore are probably not indigenous. Of the remaining 19 wheats 4 (21%) are Ne_1-carriers (allele not identified) and 15 (79%) non-carriers. This suggests that Mandchuria is also a non carrier area and probably links with Trans-Baykal and Mongolia.

We have only one wheat reported to come from West China, viz. Chinese 166. It is a non-carrier.

Non-carrier area 4 extends upto East China and Japan. TSUNEWAKI et al. (1972) identified 90 varieties from the provinces Hopeh, Shantung and Kiangsun, as 41 (46%) Ne_1-carriers, 6 (7%) Ne_2-carriers and 43 (48%) non-carriers. The Ne_2-carriers occured in Hopeh (with capital Peking) (2 vars.) and in the coastal province Shantung. They may derive from US imports during a famine in 1932 (SHEN, 1933). In adjacent more interior provinces no Ne_2-carriers were found. In these provinces 12 Ne_1- and 15 non-carriers were identified. When excluding the Ne_2-carriers, in East China 53 (48%) Ne_1-carriers and 58 (52%) non-carriers are found. Unfortunately, TSUNEWAKI et al. (1972) did not identify the Ne_1-allele, so we do not know how many of the Ne_1-carriers possess $Ne_1{}^w$ and how many $Ne_1{}^m$. My own data for the whole of China are 4 $Ne_1{}^m$-, 4 $Ne_1{}^w$- and 9 non-carriers.

Bread wheats arrived in Japan in 300 B.C. (KIHARA, 1969). At present we find non-carriers, $Ne_1{}^w$-, $Ne_1{}^m$ and Ne_2-carriers in Japan. According to TSUNEWAKI & NAKAI (1965) the Ne_2-carriers were recently imported from USA and Europe. These imports may also have included some of the non-carriers.

We do not know which Ne/ne-genotype of bread wheat reached Japan first. But, as there the three main types are found, it is possible that these three types had reached East China, after which they were simultaneously introduced into Japan.

Two bread wheat varieties from the Philippines were tested; both are non-carriers. Also two varieties from Taiwan were investigated; one is a non-carrier.

6.5.5.3.2. Ne_1^{w}*-area 2.*

The Ne_1^{w}-allele probably arose in South Iran (map 2). The Ne_1^{w}-bread wheats were later taken to North Pakistan and India (Lein's Indian wheat morpho-group, see 6.5.5.2) and from there through South China to east coast, (SHEN & KING, 1958). Two local wheats from Taiwan were tested : 1 Ne_1^{w}, and 1 non-carrier. In Japan 2 of the 27 tested varieties were Ne_1^{w}-carriers. This means that from the east coast of China Ne_1^{w}-wheats were taken to Taiwan and Japan. In Japan they are in the minority, the reason of which probably lies in the fact that they were introduced after other wheats had reached that country.

Sphaerococcum is an Ne_1^{w}-carrier. This wheat dates from ca 2500 B.C. (VISHNU-MITTRE, 1974). It has been found in the Sind valley Harappan culture (2300-1700 B.C.). Later it was taken into Madhya Pradesh (Central Prov., India) and further into Meharahtra and Bengal. In this area the Ne_1^{w}-allele is common among the land varieties. According to ELLERTON (1939) *sphaerococcum* was grown in East Baluchistan (Pakistan) and the Sind, Punjab, Madhya Pradesh and Uttar Pradesh (United Provinces) (India). It is not found at present in the Ne_1^{w} area of China. Therefore, I assume that in an early Ne_1^{w} wheat the *sphaerococcum* mutation occured after Ne_1^{w}-wheat had moved eastwards. So the Ne_1^{w}-allele is older than the s *(sphaerococcum)* allele (ZEVEN, 1978). The oldest *sphaerococcum* wheats date from 2300 B.C. so the Ne_1^{w} allele arose before that time.

The *sphaerococcum* wheat has been in cultivation upto the present time. This proves that a wheat population may stay in a certain region for some 4500 years. It supports the conclusion that most of the non-carrier wheats of the Old World derive from the first introduction of wheat together with agriculture (ZEVEN, 1979).

6.5.5.3.3. Ne_1^{m}*-area.*

The Ne_1^{m}-area of Asia links through the Arabian Peninsula with that of the Sahara and Sudan zone (map 2). Therefore, the Ne_1^{m}-bread wheats like non-carrier wheats cover an extremely large area. They must have originated probably somewhere in (Trans)Caucasia - North Iran, so in the centre of origin of bread wheat.

Ne_1^{m} bread wheats have been identified in China, but the region is not known to me. They have also been found in Japan. They must have reached this country through China probably by the route through North and Central China. Simultaneously or not, they may have been introduced together with non-carrier bread wheat.

7. *CONCLUSIONS AND SUGGESTIONS FOR FURTHER RESEARCH*

The «present» geographical distribution of the Ne-genes and their alleles shows for many parts of the Old World by which routes of bread wheat migrated and at what time this occured. However, there are many vague points which need further investigation.

The best way is to use the land varieties which were collected for the above investigation. This collection could be screened for other genes and their alleles and their geographic distribution. These genes should be neutral and not linked to genes with a strong gene x environment interaction. Such genes could be the D-genes for hybrid dwarfness (HERMSEN, 1967), but one D-gene is linked to an Sr-gene for stemrust resistance. Furthermore, the crossing work is quite laborious.

In the Introduction I have already suggested the identification work for the spring habit gene Vrn-3. Maybe this work could also cover other Vrn-genes.

Recently it became known that genes conditioning the various gliadins in wheat grains are not influenced by environment (AUTRAN, 1973). Therefore, a start was made to investigate the geographic distribution of gliadin patterns. But, when 10 grains of the externally uniform Alpine land variety Haunsberg from Austria were investigated 8 gliadin patterns were discovered. This is interesting because although this variety has been grown for some 6000-7000 years i. e. generations there is still a high genetic variation present. This shows that gliadin patterns cannot easily be used to characterize land varieties.

More work has to be done to verify the above described routes by which bread wheat spread over the Old World.

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Abstract

La dispersion du blé tendre dans l'ancien monde depuis le néolithique selon les indications du génotype produisant les nécroses d'hybrides. L'auteur a étudié la présence et la fréquence de deux gènes produisant une nécrose en hybridation dans les blés de pays d'Europe, du Proche-Orient et d'Extrême-Orient. Il en tire en conclusion les voies de dispersion du blé tendre.

novembre 1979

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