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Taxonomic and evolutionary implications of the Endosperm Balance Number hypothesis in potatoes

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Summary. The Endosperm Balance Number (EBN) hypothesis can explain to a considerable degree the crossability between tuber-bearing *Solanum* species. It has been shown to be genetically controlled and is dosage dependent. There is a good correlation between EBN and the postulated evolution and present taxonomy of potatoes. The primitive white stellate-flowered species from Mexico are 1EBN, and this condition is also found in species from South America with flowers of the same colour and shape. The evolution of a rotate corolla seems to be correlated with 2EBN. It is postulated that the 2EBN state arose as a reproductive isolating mechanism in South America. The taxonomic and evolutionary implications of the EBN hypothesis are discussed.

Key words: Potato – *Solanum* – Endosperm Balance Number (EBN) –Taxonomy – Evolution

Introduction

From the first decades of this century potato breeders have come to value more and more the important genetic characters of disease and pest resistance to be found in the wild species, which are to a greater or lesser extent related to the cultivated potato, *Solanum tuberosum*. The wide geographical extension of these wild species throughout the Americas from the USA southwards to southern Chile and their extraordinary range of ecological adaptation have intrigued both breeders and taxonomists. Indeed, the potao is a crop with possibly a wider range of genetic diversity in related wild species than any other cultivated plant. A total of 228 wild species have been described (Hawkes 1990), a large number of which can be crossed with cultivated ones. Thus, much success has been attained in transferring resistances to fungi, bacteria, viruses and various insect pests into the potato crop (Ross 1986).

Nevertheless, some of the most promising resistant wild species had until recently proved extremely difficult, if not impossible, to cross with the cultivated *S. tuberosum*. Even though there has been much field collecting and storage of materials in gene banks, with subsequent screening for the presence of a wide range of resistance characters, the intransigence of these particular wild species largely prevented their use by breeders. Certainly interspecific crossability barriers often exist between ploidy levels which encompass diploid, triploid, pentaploid and hexaploid potato species, based on $x=12$. Even so, these crossability barriers could not generally be explained by reference to differences in ploidy level, since crosses are frequently quite easy between ploidies, but not necessarily within them. Apparently insuperable barriers seemed to exist, particularly between the Mexican diploid species on the one hand and the South American diploids as well as polyploids in both subcontinents, on the other.

This was the situation up to about 15 years ago, when Den Nijs and Peloquin (1977) proposed a new hypothesis related to the role of the endosperm in obtaining interspecific crosses in potatoes.

The Endosperm Balance Number hypothesis

It has of course been known for some time that many crosses fail in both inter-polyploid and intra-polyploid crosses due to the premature collapse of the endosperm, which normally needs a

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** *Present address:* International Rice Research Institute, P.O. Box 933, 1099 Manila, Philippines ratio of two female to one male chromosome sets for satisfactory development. Den Nijs and Peloquin (1977) assumed that each chromosome set has one endosperm Balance Factor (EBF), and so in a successful cross between diploid species the endosperm would possess two female EBF: one male EBF, and hence be triploid. They went on to describe that in 4x female × 2x male crosses the EBF would be 4:1, whilst in 2x female × 4x male crosses the ratio would be 1:1. Thus, in neither case does a triploid endosperm develop, and therefore the crosses fail, unless 2n gametes function from the diploid parent, in which case the development is normal. The explanation of the lack of normal crossability between *S. acaule* (4x) or the Mexican Longipedicellata species (4x) on the one hand and *S. tuberosum* (4x) on the other can be explained by postulating an EBF of 2, rather than 4 for these wild species. This is confirmed by the ease of crossing these postulated 2EBF species with South American diploids, even though the progeny are triploid.

In the following year Johnston and Hanneman (1978) carried the matter further, though at that time they were looking for an EBF of zero to account for the crossing behaviour of *S. cardiophyllum*. This Mexican diploid species could be crossed with South American diploids only after its chromosome number was doubled. Hexaploid species (*S. demissum*, *S. oplocense*, *S. albicans* and a synthetic c-hexaploid of *S. stenotomum* × *S. stoloniferum*) were allocated an EBF number of 4 in accordance with the fact that they would cross readily with *S. tuberosum* subsp. *andigena* and the c-tetraploid derived from the diploid *S. chacoense*.

The hypothesis was further elaborated by Johnston and Hanneman (1980a, b), when the acronym EBF was discontinued and replaced by EBN (Endosperm Balance Number), now universally used. Many more species were brought into the crossing programme, and were assessed by the success or otherwise of their crosses with standard species of known EBN, namely, *S. cardiophyllum* (1EBN), *S. commersonii* (1EBN); *S. chacoense* (2EBN); *S. phureja* (2EBN); and *S. tuberosum* spp. *andigena* (4EBN) (Hanneman 1983). It was further assumed that each species or hybrid tested with an EBN less than its ploidy level probably possesses genome differentiation and should show disomic inheritance. When viable seeds resulted from a cross where they would not be expected, it was shown that these were due to the functioning of 2n gametes.

Further publications (Johnston et al. 1980; Johnston and Hanneman 1981, 1982; Hanneman 1983; Ehlenfeldt and Hanneman 1984; Hanneman 1985) provided additional evaluation of the EBN hypothesis, bringing into focus the concept of "effective polyploidy" rather than "actual polyploidy" as a clear guide to whether a proposed cross would be a success or a failure. They established that the Mexican diploids (apart from the 2EBN *S. verrucosum*) were all 1EBN, whilst the South American diploids (apart from *S. commersonii*, *S. brevidens* and *S. fernandezianum* with 1EBN) all possessed 2EBN. Later, the apparently anomalous South American diploids *S. chancayense* and *S. mochiquense* were also found to have an EBN of 1. In the Sturgeon Bay Inventory of the USDA IR-1 potato collection (Hanneman and Bamberg 1986) some 75 species were allotted appropriate EBNs as a result of extensive crossability studies (Table 1).

Further results published by Chávez et al. (1988b, c) showed that certain other South American diploids were also 1EBN, namely *S. lignicaule* and *S. capsicibaccatum*. Thus, the 1EBN species were clearly not limited to Mexico, but included the above species, as well as *S. commersonii* and the Series Etuberosa species *S. brevidens*, *S. etuberosum* and *S. fernandezianum*.

EBN results published up to 1990 were presented in the taxonomic treatment of Hawkes (1990). No doubt others will be assessed, and three is good evidence that *S. circaeifolium* is also 1EBN (Hawkes and Hjerting 1989). This is not surprising, since it belongs to the same taxonomic series, Circaeifolia, as *S. capsicibaccatum*.

Despite the apparent predictive nature of the EBN hypothesis, other crossability anomalies do exist between different potato species, both within and between ploidy levels. Even though a 2:1 EBN ratio can be postulated for the success of many interspecific crosses, seed abortion does occur in others where the 2:1 ratio is apparently satisfied. Furthermore, the reproductive isolation between species may be pre-zygotic, and crosses fail either because the pollen does not germinate on the stigma, or pollen tubes do not reach the ovary. This is certainly the case in crosses at the tetraploid level between Longipedicellata species (2EBN) and *S. tuberosum* (4EBN) (Clugston 1988).

The success of a cross may also be genotype specific. In 4x × 2x crosses between *S. tuberosum* subsp. *tuberosum* and diploid hybrids, Hanneman and Peloquin (1968) confirmed the existence of a "triploid block" (Marks 1966). When similar crosses were carried out between *S. tuberosum* subsp. *andigena* and primitive diploid cultigens such as *S. stenotomum* in the Andes, a higher frequency of triploid progeny was recovered (Jackson et al. 1978). On the basis of the EBN hypothesis these crosses should fail. However, Hermsen (1984) has pointed out the need to assess crossability between two species using a range of genotypes under varying environmental conditions.

It has also been reported by Chávez et al. (1988a) that the EBN hypothesis cannot explain the success of crosses between complex hybrids. Fertilization of putative 2n eggs from tetraploid *S. acaule*, which should be 4EBN, with normal 1n pollen of 4x hybrids between *S. etuberosum* and *S. pinnatisectum* (2EBN) is expected to result in nonfunctional endosperm, and the appearance of 6x hybrids between these three species seems to violate EBN rules.

Results and discussion

Genetic basis of the Endosperm Balance Number hypothesis

The predictive value of the EBN hypothesis is immense, and clearly opens up a new way of using wild species germ plasm in potato breeding (Ehlenfeldt and Hanneman 1984; Hanneman and Ehlenfeldt 1984). But what is the genetic basis of this phenomenon?

Some attempts to understand the genetic system behind the EBN hypothesis were made by Ehlenfeldt and Hanneman (1988) through the analysis of a complete diallel of exceptional *S. commersonii* – *S. chacoense* (1½EBN) hybrids and backcrosses to parental species. They proposed a model for the system regulating endosperm development. The model assumed that there were three unlinked homozygous loci within these species, each possessing an equal additive effect. Furthermore, the genes of *S. chacoense* apparently possess twice the effect with respect to endosperm regulation than those of *S. commersonii*. However, Ehlenfeldt and Hanneman (1988) also stated that the system as a whole exhibits a unique balance of quantitative and qualitative action because it is a system that is more ratio dependent than dosage dependent.

The similarity of the genetic systems controlling the EBN in the Mexican diploid and tetraploid species on the

Table 1. Potato species grouped by Endosperm Balance Number and ploidy levels (based on Hanneman and Bamberg 1986; Chávez et al. 1988 b, c)

Geographical distribution	1EBN	2EBN		4EBN	
	2x	2x	4x	4x	6x
United States	*jamesii*		*fendleri*		
Mexico	*brachistotrichum* *bulbocastanum* *cardiophyllum* *jamesii* *pinnatisectum* *trifidum*	*verrucosum*	*agrimonifolium* *fendleri* *hjertingii* *oxycarpum* *papita* *polytrichon* *stoloniferum*		*brachycarpum* *demissum* *guerreroense* *hougasii* *iopetalum*
South America	*brevidens* *capsicibaccatum* *circaeifolium* *chancayense* *commersonii* *etuberosum* *fernandezianum* *lignicaule* *mochiquense*	*abancayense* *amabile* *acroglossum* *ambosinum* *berthaultii* *boliviense* *brevicaule* *bukasovii* *canasense* *chacoense* *chomatophilum* *gandarillasii* *gourlayi* (2x) *huancabambense* *infundibuliforme* *kurtzianum* *laxissimum* *leptophyes* *marinasense* *medians* *megistacrolobum* *microdontum* *multidissectum* *multiinterruptum* *pampasense* *pascoense* *phureja* *raphanifolium* *sanctae-rosae* *sogarandinum* *sparsipilum* *spegazzinii* *stenotomum* *tarijense* *venturii* *violaceimarmoratum* *weberbaueri*	*acaule* *colombianum* *sucrense* (?) *tuquerrense*	*gourlayi* (4x) *sucrense* (?) *andigena* *tuberosum*	*albicans* *moscopanum* *oplocense* (6x)

one hand and South American *S. commersonii* on the other has been revealed by Bamberg and Hanneman (1990) through a series of crosses between these species and 1, 2, and 4EBN standard testers.

Taxonomic and evolutionary relevance of the EBN hypothesis

Taxonomic system. The present taxonomic system established by Hawkes (1989, 1990) seems to throw some light on the meaning of the EBN hypothesis (Table 2). This system is based on the assumption that the Mexican diploid potatoes with white stellate corollas possess a number of primitive characters such as a two-band or even one-band serological spectrum when tested against *S. tuberosum* antiserum, whilst all other wild potato species produce a four-to-five-band spectrum (Gell et al. 1960).

Hosaka et al. (1984), working on restriction endonuclease analysis of chloroplast DNA, also grouped the Mexican white stellate-flowered species separately from

Table 2. Taxonomic groupings of *Solanum* Sect. *Petota*, Endosperm Balance Numbers and geographical distribution

Subsections	Superseries (corolla groups)	Series	Ploidy[1]	EBN	Geographical distribution
Estolonifera		*Etuberosa*	2x	1	South America
		Juglandifolia	2x	?	
Potatoe	*Stellata* (Primitive)	*Morelliformia*	2x	1	South-Western USA, Mexico Central America
		Bulbocastana	2x	1	
		Pinnatisecta	2x	1	
		Polyadenia	2x	1	
		Lignicaulia	2x	1	South America
		Circacifolia	2x	1	
		Commersoniana	2x	1	
		Olmosiana	2x	?	
	Stellata (Advanced)	*Yungasensa*	2x	2	South America
	Rotata (Primitive)	*Cuneoalata*	2x	2	Southern to central regions of South America
		Negistacroloba	2x	2	
		Southern forms of *Tuberosa*	2x, 4x, 6x	2, 4	
		Southern forms of *Conicibaccata*	2x	2	
	Rotata (Advanced)	*Piorana*	2x, 4x	2	Central to northern regions of South America
		Ingifolia	2x	?	
		Acaulia	4x, 6x	2, 4	
		Central and northern forms of *Tuberosa* and *Conicibaccata*	2x, 4x, 6x	(1), 2, 4	
		Longipedicellata	4x	2	South-Western USA Mexico, Central America
		Demissa	6x	4	
		Mexican forms of *Conicibaccata*	4x	2	

[1] Not including odd polyploid cytotypes found in some species

others, but linked them distantly, though on the same branch, with *S. etuberosum*. All these species are 1EBN (Table 1). More recently, Debener et al. (1990) have evaluated the phylogeny of wild and cultivated Solanums based on the analysis of nuclear RFLPs. The link between *S. etuberosum* and *S. polyadenium* and *S. pinnatisectum* was confirmed. There was also a closer relationship between these species and *S. stoloniferum*, a 4x (2EBN) species also from Mexico, than with the South American Tuberosa diploids and tetraploids (2EBN or 4EBN) or 6x *S. demissum* (4EBN) from Mexico. The phenetic trees given by Debener et al. (1990) generally supported the descriptions of relationships among *Solanum* species based on biosystematic studies, with the exception of *S. chacoense* and *S. megistacrolobum*.

It was postulated (Hawkes 1988, 1990) that the origin of the tuber-bearing group occurred in Mexico and that some of these species may have migrated to South America in early Pliocene times (Fig. 1). Possible remnants of this migration with white stellate flowers are *S. lignicaule* in Peru, *S. capsicibaccatum* and *S. circaeifolium* from Bolivia and *S. commersonii* from Argentina, Uruguay and Brazil. These are all 1EBN species, though it should be stated that their chloroplast DNA groups with the 2EBN species. Somewhere, in Argentina perhaps, the 2EBN condition evolved, probably in another more vigorous diploid group of species (Series Yungasensa), which includes *S. chacoense* and *S. tarijense*. At some later date the rotate-flowered 2EBN diploids were derived from the stellate-flowered 2EBN species, and these spread northwards, finally even returning to Mexico across the Central American isthmus where the 2EBN species *S. verrucosum* in Mexico can be seen.

It must be conceded, however, that two anomalous 1EBN diploid species with rotate corollas occur in Peru, namely *S. chancayense* and *S. mochiquense*. Even though they possess white flowers, they still cannot easily be fitted into the scheme as outlined above, unless we assume that the rotate corolla has evolved independently in these species. They still retain the primitive 1EBN feature, whilst in the rest of the diploid species the 1EBN condition was lost before the rotate corolla evolved.

Further information is clearly needed on the Endosperm Balance Number of many other diploid white-flowered Peruvian species such as *S. olmosense* (stellate corolla), *S. contumazaense*, *S. jaenense*, *S. cantense*, *S. hypacrarthrum*, *S. raquialatum*, *S. gracilifrons*, *S. immite* and *S. incahuasinum*. Other white-flowered species of un-

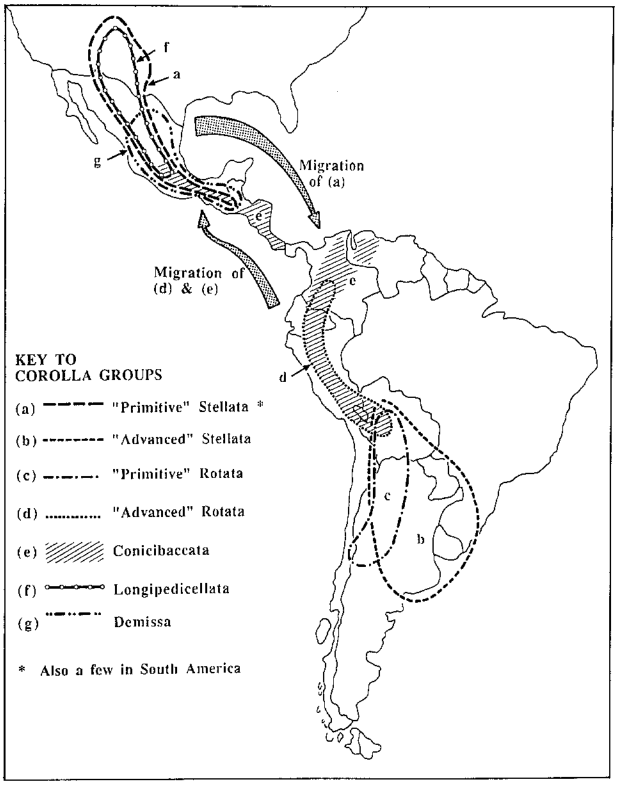

Fig. 1. Probable migration routes and geographical distribution of corolla groups in potato species (modified from Hawkes 1988)

known chromosome number might also be investigated when material becomes available.

Ploidy levels. It is interesting to reflect that apart from the fact that diploid species may by 1EBN or 2EBN, the tetraploids may be 2EBN or 4EBN (Table 1). The 2EBN tetraploids possess bivalent pairing, as pointed out by Johnston et al. (1980). In fact, we have seen that all of the apparent allotetraploids so far investigated are 2EBN species. These include species in Series Acaulia (*S. acaule*), Series Conicibaccata (such as *S. colombianum*, *S. oxycarpum*), Series Longipedicellata (such as *S. stoloniferum*, *S. fendleri*) and Series Piurana (*S. tuquerrense*).

The 4EBN species *S. tuberosum* (and its subsp. *andigena*) is generally thought to be a cytological autotetraploid or an auto-allotetraploid, even though it was probably derived as a tetraploid progeny from two nearly related diploids (Cribb and Hawkes 1986). Other 4EBN tetraploids are *S. gourlayi* (4x cytotype) and *S. sucrense*. The former could easily be an autotetraploid or a hybrid between two closely related species of similar genome composition. However, *S. sucrense* seems to have a complex ancestry and is a probable cross between *S. tuberosum* subsp. *andigena* (4EBN) and a tetraploid form of *S. oplocense* whose EBN has not yet been ascertained (Astley and Hawkes 1979). From our own studies of the crossability of *S. sucrense* with diploid 2EBN species, there is some evidence to indicate that it could also be 2EBN. At the present time all of the hexaploids known are allopolyploids, with an EBN of 4. They occur in Series Acaulia, Demissa, Conicibaccata and Tuberosa.

It would seem from the rather sparse evidence available that the EBN of autopolyploids is a sum of their genome components, whilst that of allopolyploids is half that of their genome components. This of course raises the problem of how the EBN could be reduced from 4 to 2 when, by differentiation, the two original genomes become distinct, if this indeed is what takes place.

Evolutionary implications. EBNs have been determined for less than 50% of the tuber-bearing Solanums (Table 1). Nevertheless, from the evidence we have at present there does seem to be a correlation between the EBN hypothesis and the postulated evolution of the tuber-bearing group of species. In other words, the 1EBN condition is found chiefly in species that are considered as close to the ancestor of the potato. These are the Mexican Series Morelliformia, Bulbocastana, Pinnatisecta and Polyadenia, all with white-stellate corollas and all 1EBN. Further back in evolutionary time they seem to be related to the South American non-tuber-bearing Series Etuberosa, but exactly how this took place is not yet known. However, the chloroplast DNA and RFLP studies of Hosaka et al. (1984) and Debener et al. (1990) clearly show a relationship, even though a distant one.

The EBN condition seems to be genetically controlled (Ehlenfeldt and Hanneman 1988; Bamberg and Hanneman 1990), but it is difficult to see at present why or how it evolved. It is certainly an isolating mechanism, as suggested by Ehlenfeldt and Hanneman (1988), but in the initial stages of potato evolution in Mexico, when all species were 1EBN, there were no 2EBN species in existence from which they needed to be isolated. We can only postulate that the 1EBN condition represented the original natural state of wild potatoes in South America and that the 2EBN condition arose in this continent at a later date as an isolating mechanism. This may have taken place in Argentina during the evolution of Series Yungasensa species (*S. chacoense*, etc.) from *S. commersonii.*

The concept of "effective ploidy" as distinct from "actual ploidy" is an extremely useful one for potato breeders. The "primitive" nature of 1EBN and the "advanced" nature of 2EBN seems reasonably correct; but why this took place and what was its real function, if any, must still be a matter for conjecture.

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