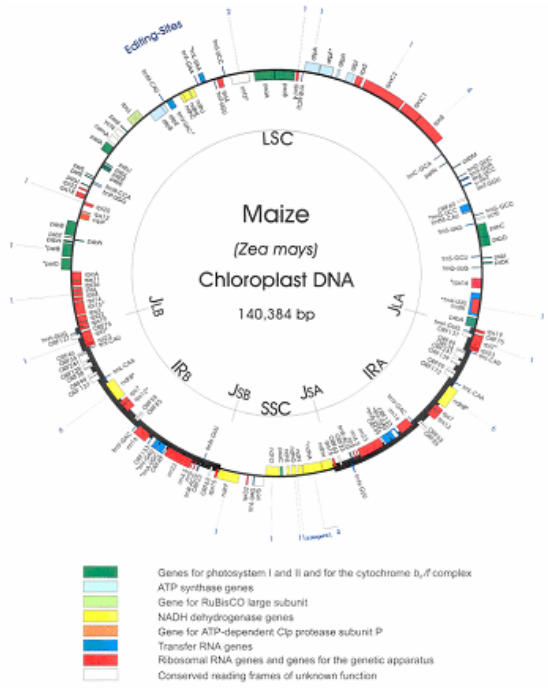
EVOLUTION AND EXPRESION OF THE *ndh* GENES

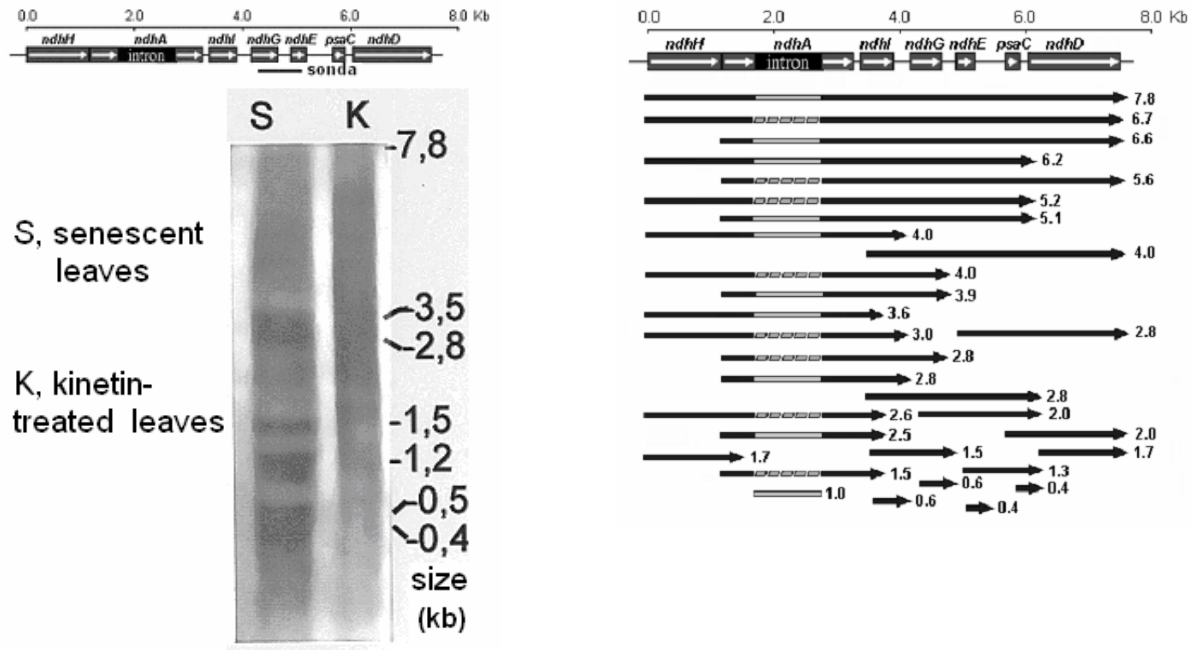
The chloroplast DNA of the most of higher plants contains 11 genes *ndh* encoding components of the multi-polypeptidic Ndh complex which is involved in the regulation of the redox level of the photosynthetic electron carriers to optimise the cyclic electron transport and photophosphorylation. The synthesis of the NDH polypeptides (encoded by the *ndh* genes) and the levels of the Ndh complex increase under photo-oxidative stress and in senescence. The development of the senescence syndrome requires the expression of the *ndh* genes which is not accompanied by an increase of the chloroplastic superoxide dismutase, therefore raising the level of reactive oxygen species and leading to cell death.



The map of maize plastid DNA shows that six *ndh* genes (yellow) (*H*, *A*, *I*, *G*, *E* y *D*) are clustered in the operon *ndhH-D* which also includes the *psaC* gene (between *ndhE* and *ndhD*) for the PsaC polypeptide of photosystem I. Three genes (*ndhC*, *ndhK* and *ndhJ*) are clustered in a second operon and *ndhB* (repeated) and *ndhF* genes probably are within independent monocistronic transcriptional units.

Chloroplast DNAs of the most of algae lack *ndh* genes as is the case of: *Cyanophora paradoxa* (Glaucophyte); *Guillardia theta* (Cryptophyte); *Cyanidioschyzon merolae*, *Cyanidium caldarium*, *Porphyra purpuea* (Rhodophytes); *Euglena gracilis*, *Euglena longa* (Euglenophytes); *Odontella sinensis* (Chromophyte) and some Chlorophytes (*Chlamydomonas reinhardii*, *Chlorella vulgaris*). In contrast, *ndh* genes are present in the chloroplast DNA of some other Chlorophytes (*Chaetosphaeridium globosum*, *Nephroselmis olivacea*, *Mesostigma viride*) and in almost all Bryophyites, Pterdophyites, Gymnosperms and Angiosperms. Some higher plants lacks *ndh* genes, among them a few photosynthetic (*Pinus koraiensis*, *Pinus thunbergii*) and all non-photosynthetic tested (*Cuscuta reflexa*, *Orobanche minor*) that usually have *ndh* pseudogenes. Probably, the presence of *ndh* genes distinguishes the Chlorophytes most closely related to the ancestors of higher plants.

Transcripts of the *ndhH-D* operon



Levels of the mRNAs of the *ndhB* y *ndhF* genes increase during senescence and in response to photo-oxidative stress. Polycistronic operons containing *ndh* genes show a complex pattern of transcripts in which the relative abundance of each one vary, usually increasing the monocystronic mRNAs during leaf senescence. Extensive investigations with the *ndhH-D* operon revealed many processing stages of the 7.8 kb primary transcript including editing of some C bases to U, splicing of the intron of *ndhA* and inter- and intra-genic nuclease cleavages.

Similarly to other plastid transcripts of higher plants, the editing of *ndh* gene transcripts modifies some C to U. The *ndh* genes include most of the editing sites of the plastidal genes of Angiosperms. Probably, *ndh* genes were dispensable in the ancestor of modern Angiosperms and accumulated a number of mutations but were not suppressed. Further lowering of atmospheric CO_2 and colonising of new lands made photo-oxidative stress conditions more frequent. These changes and the emergence of station leaf fall behaviour could favour the functional rescue of *ndh* genes. The rescue was carried out by C to U editing only in plants where the previous mutations changed T to C in DNA and affected the coding of critical amino acids. Later, during Angiosperm evolution, editing sites are being lacked by retro-mutation C to T at the genome level.

Little is known about the editing machinery and the order and control of the polycistronic transcript processing in chloroplasts. Almost all required sites are C to U edited early during the processing of the primary transcript of the *ndhH-D* operon. One exception is the site III of the *ndhA* gene which is only edited after intron splicing. In fact, a number of transcripts contain the *ndhA* intron and all sites edited except site III which map in the exon2 near the intron. Structural predictions indicate that in the typical secondary structure required for the splicing of type II intron the C of site III base paired with a G. Only after intron splicing that C become free and is edited to U. In some way, the requirement of C at site III for intron splicing has prevented the genomic retro-mutation of site III C to T in many plants.

Chloroplats contain 100 to 200-folds higher level of the PsaC polypeptide (component of photosystem I) than of NDH polypeptides. To do so, appropriate mechanisms allow the accumulation of the monocistronic transcript of the *psaC* gene in detriment of the levels of *ndh* gene transcripts. During the processing of the primary transcript of the *ndhH-D* operon, the mature *psaC* mRNA is stabilized because it is 3´-end enlarged to include sequences of the following *ndhD* gene in the operon. Therefore, the fraction of primary transcripts leading to stable *psaC* mRNA decreases the yield of mature translatable mRNA of the *ndhD*. Obviously, thorough investigations of the processing of the transcripts of the *ndhH-D* operon will allow to know the control of the expression of ndh genes and, in general, the post-transcriptional control in chloroplasts.