20

From Seed to Tree: The Functioning and Evolution of DNA Repair in Plants

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1. Introduction

In order to alleviate harmful effects of DNA damage and maintain genome integrity, all living organisms have developed a complex network of DNA repair mechanisms. However, the biochemical and genetic studies of DNA repair pathways have hitherto focused mostly on bacterial, yeast and mammalian systems (Sancar et al., 2004; Pan et al., 2006; Goosen & Moolenaar, 2008; Jackson & Bartek, 2009), whereas plants have been somewhat neglected in this respect. In plant cells, DNA damages can be generated "spontaneously" by reactive metabolites and by mistakes that occur during DNA replication and recombination processes or they can arise from exposure to environmental DNA damaging agents (Tuteja et al., 2001 & 2009). Plants are sessile organisms, which are continuously exposed to a wide variety of biotic and abiotic stresses, which can cause DNA damages directly or indirectly via the generation of reactive oxygen species (ROS) (Roldán-Arjona & Ariza, 2009). In plants, mutations, which initially arise in somatic cells, may also be present in gametes because plants lack a reserved germline and produce meiotic cells late in development (Walbot and Evans, 2003). However, the mutation rate in long-lived coniferous forest trees, such as pines, is not unexpectedly high, which indicates that the activities responsible for maintaining genome integrity must be efficient in somatic cells (Willyard et al., 2007).
This chapter gives an overview of the special requirement of DNA repair in plants particularly from the point of view of longevity and the lifestyle of plants. We introduce the sequences of the Scots pine (*Pinus sylvestris* L.) putative *RAD51* and *KU80* genes which are involved in the repair of double-strand breaks (DSBs) by homologous recombination (HR) and non-homologous end-joining (NHEJ), respectively. The novel sequence data is used in the reconstruction of the evolutionary history of the *RAD51* and *KU80* genes in eukaryotes. In addition, the use of the HR and NHEJ pathways is demonstrated during the Scots pine seed development. From its early stages of development in the mother plant onwards, a pine seed is exposed to developmentally programmed as well as environmental stresses which are potentially damaging to the genome. Furthermore, the pine seed represents an interesting inheritance of seed tissues as well as anatomically well-described sequences of embryogenesis. Thus, we consider the pine seed to be a model system for studying the DNA repairing mechanisms, yet not solely within plants, but in wider use – for eukaryotes in general.

2. Searching for a fountain of youth in pines

Organismal ageing is generally connected to deterioration. With the passage of time, organisms accumulate stochastic damage to DNA, proteins and other macromolecules (Rattan, 2008). If damages are left unrepaired, they impair important biological functions and, furthermore, result in age-related physiological changes, an increased susceptibility to diseases and environmental stress, reduced fertility, and finally, to increased mortality (Watson & Riha, 2011). The rate of damage accumulation should be approximately equal in all organisms. However, both the rate of senescence and the length of lifespan vary largely among organisms, which suggests that they are genetically determined (Finch, 2001).

Plants have adopted many survival strategies that are totally different from those of animals, and in relation to plants, even the terms individual, aging and lifespan may sometimes be difficult to define (Thomas, 2002; Munné-Bosch, 2007). Furthermore, vegetative propagation is common in plants, and even entire forests can consist of one tree clone. In quaking aspen (*Populus tremuloides* Michx.), clones are formed by sprouting of stems from the root systems of aspens that originally are derived from a seed (Lanner, 2002). The development of plants differs completely from the development of animals, which must be taken into account in inquiries into age-related changes in plants. In plants, only a fundamental body plan is established during embryogenesis, and practically all structures and organs are formed by the proliferation of meristematic cells throughout adult life (Watson & Riha, 2011). In plants, new organs develop asynchronously during a plant's life and these have shorter lifespans than the plant as a whole (Aphalo, 2010). Concerning plant ageing, it is essential to underline that senescence can also be a highly regulated physiological process, such as a development-related physiological cell death, which is significant when compared to the death of the whole organism. In annual plants, leaf senescence is connected with the death of the whole plant, whereas in perennials, leaf senescence is a regulated physiological process that contributes to nutrient recycling and allows the rest of the plant to benefit from the nutrients which have accumulated in leafs (Lim, 2007). In trees, the biomass may mostly consist of dead cells that form a supporting structure for a thin layer of newly emerged organs (Watson & Riha, 2011).

A walk through a park is enough to show that plants age as well and that the rate of senescence and the length of lifespan are species-specific. Plants can live from a few weeks to as long as millennia (Thomas, 2002; Lanner 2002). Monocarpic plants flower, set seed and die. The monocarpic habit is well exemplified by the model plant *Arabidopsis thaliana* (L.), which may go through its entire life cycle in 8 to 10 weeks, but may nevertheless produce thousands of offspring during that time (Hensel et al., 1993). In association with massive reproductive effort, the leaves, stems and fruits of the adult Arabidopsis plant undergo progressive senescence that ultimately results in the death of the plant (Hensel et al., 1993). Despite the fact that Arabidopsis is considered to be a mere weed, due to its small size, small genome, quick generation time, ease of genetic transformation, and the availability of mutant plants, it has been found to be useful both as a model for plants in general and for the study of a variety of fundamental biological processes (Meyerowitz, 1989; Swarbreck et al., 2008). In contrast to Arabidopsis, trees are examples of long-living organisms. Trees usually remain reproductive into great old age, and hence, the characteristics that prolong life are thought to be naturally selected because they increase fitness by multiplying reproductive opportunities (Lanner, 2002). In fact, the oldest living individual organism known on earth is a tree – a Great Basin bristlecone pine (*Pinus longaeva*), which has attained

at least 4862 years (Lanner, 2002). While several Great Basin bristlecone pines have exceeded 4000 years of age, they do not show evident signs of senescence (Lanner & Connor, 2001). The grafting experiments with Scots pine indicated that age-related regulation in the growth is mainly caused by physical factors and not by the age itself (Vanderklein et al., 2007).Thus, the lifetime of trees seems to be mostly limited by external factors such as the activities of pests, the frequency and intensity of fires, and ultimately, by how long it takes for the soil to erode away from their roots (Lanner, 2002).

The two major groups of seed plants, angiosperms and gymnosperms, shared a common ancestor approximately 285 million years ago (Bowe et al. 2000). For several decades, Arabidopsis has provided the leading model for angiosperms (Meyerowitz, 1989), whereas pines, *Pinus* species, have been suggested as a model for gymnosperms and woody plants (Lev-Yadun & Sederoff 2000). The genus *Pinus* has a rich history of phylogenetic analysis, and the relationships between the approximately 120 extant species are well documented (Gernandt et al. 2005), as are the development, reproduction, ecology and genetics of many pine species (Lev-Yadun & Sederoff 2000). Although pines and other gymnosperms are generally considered to be difficult subjects for genetic studies e.g. due to their long generation times, large genome size and outbred mating system, they have one remarkable advantage: the haploid megagametophyte tissue represents a single meiotic product and makes the direct analysis of inheritance of genetic loci possible without the use of controlled crosses (Devey et al. 1995). Five pines were ranked to be the most interesting on the basis of their biological, geographical or economical importance. The economically dominant pines are loblolly pine (*P. taeda*), Monterey pine (*P. radiata*) and Scots pine (Lev-Yadun & Sederoff 2000). Scots pine is the most widely distributed Eurasian conifer and one of the keystone species in the Eurasian boreal forest zone, growing in a range of environments from Spain and Turkey to the subarctic forests of northern Scandinavia and Siberia (Mirov, 1967). Additionally, two bristlecone pines, *P. aristata* and *P. longaeva*, were selected to the top five due to their greatest longevity (Lev-Yadun & Sederoff 2000). Several reports have suggested that the activities responsible for the maintenance of genome integrity must be efficient in pines. Despite the long lifetime, the observed mutation rates in the somatic cells of pines were not unexpectedly high (Willyard et al., 2007). Furthermore, no age-dependent decline was detected in the telomeres of extremely long-lived bristlecone pines, although a positive correlation was found between telomere length and life expectancy in a study in which six tree species were compared (Flanary and Kletetschka, 2005). The results suggested that answers to many intriguing questions about the maintenance of genomic integrity during organismal ageing may be found in pine trees.

3. A future vision: From weed to seed

The seed represents the main vector of plant propagation and thus, in a plant's life, it is a critical stage with many special characteristics (Rajjou & Debeaujon, 2008). According to the practical instructions for plant seed storage (Bonner, 2008), plant seeds can be classified into five types: true orthodox, sub-orthodox, intermediates class between orthodox and recalcitrant (Ellis et al. 1990), temperate recalcitrant, and tropical-recalcitrant. The seeds of most tree species with high economic value (e.g. *Abies*, *Betula*, *Pinus, Picea*) at the Northern Temperate Zone as well as many tree species (e.g. *Cauarina, Eucalyptus, Tectona*) at tropics and subtropics are true orthodox. The water content of a seed is determined by seed composition and, in addition, it is in equilibrium with the prevailing relative humidity.

Orthodox seeds are able to withstand the reduction of moisture content to around 5% (Berjak & Pammenter, 2002) and they can be stored for long periods (10 to 50+ years) at subfreezing temperatures (Bonner, 2008). Embryo development, reserve accumulation and maturation / drying are the three typical stages of orthodox seed development, leading from a zygotic embryo to a mature, quiescent seed. The maturation drying causes severe stress, and a wide range of mechanisms such as protection, detoxification and repair are needed for the surviving of a seed during the dry state and to preserve the high germination ability (Buitink & Leprince, 2008; Rajjou & Debeaujon, 2008). The longevity of seeds during storage has a major ecological, agronomical as well as economical importance (Rajjou & Debeaujon, 2008), and seed conservation is one of the useful strategies to conserve plant genetic diversity (Cochrane, 2007). Furthermore, the seeds of particular plant species such as canna (*Canna compacta*), sacred lotus (*Nelumbo nucifera* Gaertn.) and date palm (*Phoenix dactylifera* L.) represent the most impressive examples of organismal longevity (Lerman & Cigliano, 1971; Shen-Miller, 2002; Sallon et al., 2008).

Seeds are subjected to DNA damage during maturation drying, but also during seed storage. Due to the fairly easy detection of chromosome breakage or translocations, DNA lesions during seed ageing has been demonstrated for a long time. As early as in 1969, it was shown that, in the seeds of crop species such as barley (*Hordeum vulgare* L.), broad bean (*Vicia faba* L.) and pea (*Pisum sativum* L.), chromosomal damages appeared as a result of the cumulative effects of temperature, moisture and oxygen during the ageing of seeds (Abdallah & Roberts, 1969). Later, the accumulation of chromosomal aberrations appeared to be a significant factor by its contribution to the loss of seed viability during storage (Cheah & Osborne, 1978). In maize (*Zea mays* L.) seed, the maturation drying / rehydration cycle creates thousands of single strand breaks (SSBs) in the genome of each cell (Dandoy et al., 1987). During germination, a seed recovers physically from maturation drying, resumes a sustained intensity of metabolism, completes essential cellular events to allow the embryo to emerge, and induces subsequent seedling growth (Nonogaki et al., 2010). Quantitative trait loci (QTL) mapping in Arabidopsis (Clerkx et al., 2004) and rice (*Oryza sativa* L.) (Miura et al., 2002) revealed that seed longevity during storage and germination is controlled by several genetic factors. In particular, the maintenance of genetic information during the seed dehydration and rehydration cycle has been found to be essential for plant survival (Osborne et al., 2002). It has been suggested that the capability to restore genetic integrity during rehydration in an embryo whose DNA is damaged is a major factor in the determining of the seed desiccation tolerance (Boubriak et al., 1997).

In seeds, DNA repair mechanisms improve emergence and germination, particularly under stress conditions. Artificially, DNA repair can be facilitated by seed priming, that is, by controlled hydration of seeds (Rajjou & Debeaujon, 2008). Due to incomplete hydration, seeds remain desiccation-tolerant and can be re-dried after treatment (Heydecker et al., 1973). For example, in *Artemisia sphaerocephala* and *Artemisia ordosia*, DNA repair during seed priming improves seed viability under harsh desert conditions (Huang et al., 2008). Although DNA repair has been demonstrated to occur during seed priming, the molecular mechanisms involved in DNA repair in seeds are still poorly known. In Arabidopsis seed, the activities of poly (ADP-ribose) polymerases (PARP enzymes) that are implicated in DNA base-excision repair are important for germination (Hunt et al., 2007). Also, DNA ligase VI (Waterworth et al., 2010) and one of the three *RAD21* gene homologues, *AtRAD21.1* (da Costa-Nunes et al., 2006), play critical roles in the recovery from DNA damage during Arabidopsis seed imbibition, prior to germination.

4. The lifestyle of plants - living hard, repairing smart

Although ageing may involve damage to various cellular constituents, the imperfect maintenance of genetic information has been suggested to be a critical contributor to ageing (Lombard et al., 2005). Thus, the necessity of appropriate and effective responses to potential mutagenic events is emphasized by several features in the plant's lifestyle which expose them to both external and internal sources of DNA damage. As sessile organisms, plants are continuously exposed to a wide variety of abiotic stresses such as infection by various pathogens, the ultraviolet (UV) component of sunlight, ozone, dehydration and wounding which may cause DNA damages directly or indirectly via the generation of reactive oxygen species (ROS) (Roldán-Arjona & Ariza, 2009). Plants and algae are the only photosynthetic eukaryotes able to capture energy from sun light. Thus, ROS are continuously produced within plant cells also as a result of normal oxidative cellular processes such as photosynthesis and mitochondrial respiration, and they may treat the integrity and viability of cells if they are not removed (Mittler et al., 2004). Oxidative stress, a situation in which ROS exceed cellular antioxidant defenses, can cause lipid peroxidation, protein damage as well as several types of DNA lesions (Lombard et al., 2005). Although ROS are toxic molecules, they also control many different processes in plants. Therefore, the level of ROS in plant cells is tightly regulated, and the intensity, duration and localization of different ROS signals are determined by interplay between the ROS production and ROS scavenging pathways (Mittler et al., 2004). Plant cells respond to persistent DNA stress by losing their competence to divide, which may lead to meristem arrest, but normally, meristems proliferate for the entire plant's lifetime which can be even millennia in some long-lived trees. That is, meristematic cells may divide thousands of times, which inevitably results in a replication-dependent loss of telomeres if their maintance is impaired (Watson & Riha, 2011).

Exogenous and endogenous genotoxic agents may produce various kinds of DNA lesions such as altered base, missing base, mismatch base, deletion, insertion, linked pyrimidines, single (SSB) and double strand breaks (DSB) as well as intra- and inter-strands cross-links (Tuteja et al., 2001). Therefore, organisms have developed a complex network of DNA repair mechanisms both to alleviate harmful effects of DNA damage and to maintain genome integrity (Hakem, 2008). In many cases, the same type of DNA lesions can be processed by several repairing mechanisms (Boyko et al., 2006). Depending on the severity and type of the DNA damage, cellular response can either be the activation of DNA repair pathways, but also a cell cycle arrest or a programmed cell death (PCD) (Barzilai et al., 2004), which indicates that DNA repair systems are tightly connected with other fundamental cellular processes. Particularly, DSBs can be extremely deleterious lesions. Even a single unprocessed DSB can cause a cell death (Rich et al., 2000) by inactivating key genes or by leading serious chromosomal aberrations (van Gent et al., 2001). On the other hand, cellular processes such as DNA replication and the repair of other kinds of DNA lesions give rise to DSBs, and thus, the consequences of DSBs are not always solely harmful to the cell (Bleuyard et al., 2006). Diploid cells can use homology-directed repair (HDR) in DSB repair. The most common form of HDR is homologous recombination (HR), which involves extensive sequence homology between the interacting DNA molecules (Lieber, 2010). In non-dividing haploid cells or in diploid cells that are not in S-phase, a homology donor is not nearby, but they can get over DSBs by non-homologous recombination (NHEJ), which acts independently of significant homology and simply rejoins the two ends of the break

(Bleuyard et al., 2006, Lieber, 2010). These two pathways have different repair fidelity: HR has been considered to be a more accurate pathway that ensures the repair of DSB without any loss of genetic information (Bleuyard et al., 2006), whereas NHEJ results in various mutations varying from single nucleotide substitutions to deletions or insertions of several nucleotides (Pelczar et al., 2003, Kovalchuk et al., 2004). However, HR has frequently found to lead to large segmental duplication, gene duplication, gene loss, or gene inactivation (Boyko et al., 2006). Thus both HR and NHEJ may have roles in genome evolution due to genome rearrangements. Especially in plants, genetic change in somatic cells is relevant for evolutionary considerations because mutations in meristematic cells can be transferred to the offspring (Walbot, 1996). Kirik et al. (2000) analyzed the formation of deletions during DSB repair in two dicotyledonous plant species, Arabidopsis and tobacco (*Nicotiana tabacum* L.), which differ over 20-fold in genome size. They found a putative inverse correlation between genome size and the average length of deletions, which suggested that species-differences in DSB repair may influence genome evolution in plants (Kirik et al., 2000). Pelczar et al. (2003) studied genome maintenance strategies of organisms belonging to different kingdoms (animals versus plants) but of similar genome size. They found that in human HeLa cells, 50–55% DSBs were repaired precisely – a high percentage when compared to as little as 15–30% in tobacco cells – and, moreover, the DSB repair in plants resulted in 30–40% longer deletions and significantly shorter insertions. The findings suggested that the strategies for DSB repair and genome maintenance may be different in plants and animals (Pelczar et al., 2003).

The molecular components of HR and NHEJ pathways are highly conserved amongst eukaryotes and both of the pathways are required for the repairing of DSB also in plants (Bray and West, 2005; Bleuyard et al., 2006). One of the central proteins in HR is RAD51, which ensures high fidelity DNA repair by facilitating strand exchange between damaged and undamaged homologous DNA segments (Baumann & West, 1998). In addition, several RAD51-like proteins such as XRCC2 appear to help with this process (Tambini et al., 2010). In the mediation of NHEJ, a DNA dependent protein kinase (DNA-PK) complex which comprises a KU70-KU80 heterodimer and a catalytic subunit (PKcs) plays a central role (Tamura et al., 2002). The key regulatory mechanisms that direct which pathway is used for DSB repair are still poorly known if they exist at all (Boyko et al., 2006). The suggestion that HR and NHEJ compete for available DNA ends at break sites is based at the molecular level on the equilibrium between RAD52 (HR) and KU70-KU80 dimer (NHEJ) in animals (Ray and Langer, 2002). However, Arabidopsis genome contains no *RAD52* homolog (Bleuyard et al., 2006), whereas *RAD51* homolog has been identified (Doutriaux et al., 1998). Thus, the availability of the key proteins, such as RAD51 and KU proteins, at the time of DSB repair may also be one of the regulatory mechanisms. In Arabidopsis, the rate of HR decreased with plant age, whereas the frequency of strand breaks and point mutations increased. These events were parallel by a decrease in the abundance of *RAD51* transcripts as well as increase in the abundance of *KU70* transcripts and KU70 protein (Boyko et al., 2006). These results of Boyko et al. (2006) suggest that the involvement of HR and NHEJ in DSB repair may be developmentally controlled in plants.

5. DNA fragmentation and repair during Scots pine seed development

As an orthodox seed, a developing pine seed goes through maturation drying during which metabolic activity is gradually reduced and the seed enters into a quiescent state. In addition

to this, the development of a viable pine seed includes the strictly co-ordinated action of several cell death programs. A characteristic feature of the Scots pine seed development is the presence of more than one embryo in the developing seed (Fig. 1A). In the beginning of the seed development, the fertilization of many egg nuclei results in several embryos of the same ovule (Buchholz 1926). Later, polyzygotic embryos undergo cleavage polyembryony (Sarvas 1962). However, only the dominant embryo survives and completes its development (Fig. 1B), while subordinate embryos, as well as suspensor tissue, are deleted by programmed cell death (PCD) during the progress of seed development (Filonova et al. 2002). Megagametophyte cells in the embryo surrounding region (ESR) die through necrotic-like cell death (Vuosku et al., 2009), and in addition, the maternal cells of the nucellar layers face destruction during early embryogenesis (Hiratsuka et al., 2002; Vuosku et al., 2009).

In a gymnosperm seed, the megagametophyte tissue develops from a haploid megaspore before the actual fertilization of the eggs (Singh 1978). The megagametophyte houses the majority of the storage reserves of a seed (King & Gifford, 1997) and provides nutrition for the developing embryo during seed development as well as for the young seedling during early germination (Fig.1C). We have shown that, in Scots pine seed, the megagametophyte tissue stays alive from the early phases of embryo development until the imbibition phase of early germination of mature seed, except for the cells in the ESR (Vuosku et al., 2009). Positive signals in TUNEL (terminal deoxynucleotidyl transferase-mediated dUTP nick end labelling) assay indicate DNA fragmentation in the nuclei of the megagametophyte cells at the late embryogeny (Fig.1D). However, the megagametophyte cells do not show other morphological signs of cell death, but appear to be viable with the active gene expression. The decreasing expression of the PCD-related metacaspase (*MCA*) and Tat-D nuclease (*TAT-D*) genes during Scots pine seed development confirms that no large-scale PCD or nucleic acid fragmentation occur in the megagametophyte tissue. Instead, the DNA fragmentation may be a consequence of DNA strand breaks caused by maturation drying or by the DNA breaks with free 3′-OH ends that appear during DNA repair. During the seed development, the expression of *RAD51* gene decrease, whereas the expression of the *KU80* and DNA ligase (*LIG*) genes remain constant, which suggests that the proportion of mitotic cells decrease and the DNA breaks are mainly repaired by NHEJ pathway (Vuosku et al., 2009).

Nuclear DNA fragmentation is currently one of the most frequently used sign of PCD. However, in the Scots pine seed, the megagametophyte cells remain metabolically active until the imbibition phase of germination despite DNA fragmentation in the nuclei already during late seed development (Vuosku et al., 2009). In plants, both the tolerance of DNA fragmentation and effective DNA repair mechanisms may be adaptations to the special energy metabolism as well as to a sessile life style which exposes cells to various endogenous and exogenous stresses. Thus, in plants, DNA fragmentation can also be a temporary process and does not always proceed to cell death.

6. Evolution of DNA repair related *recA/RAD51* gene family and *KU80* gene in eukaryotes

Previously, the homologs of both *recA* and *RAD51* genes have been identified from several prokaryotes and eukaryotes (Eisen, 1995; Bishop et al., 1992; Shinohara et al., 1992). In Arabidopsis, nuclear genome codes four recA-like proteins, RECA1, RECA2, REC3 and DRT100 that have been located in mitochondria and chloroplasts (Cao et al., 1997; Pang et al., 1992; Shedge et al., 2007). In addition to RAD51, Arabidopsis genome encodes seven

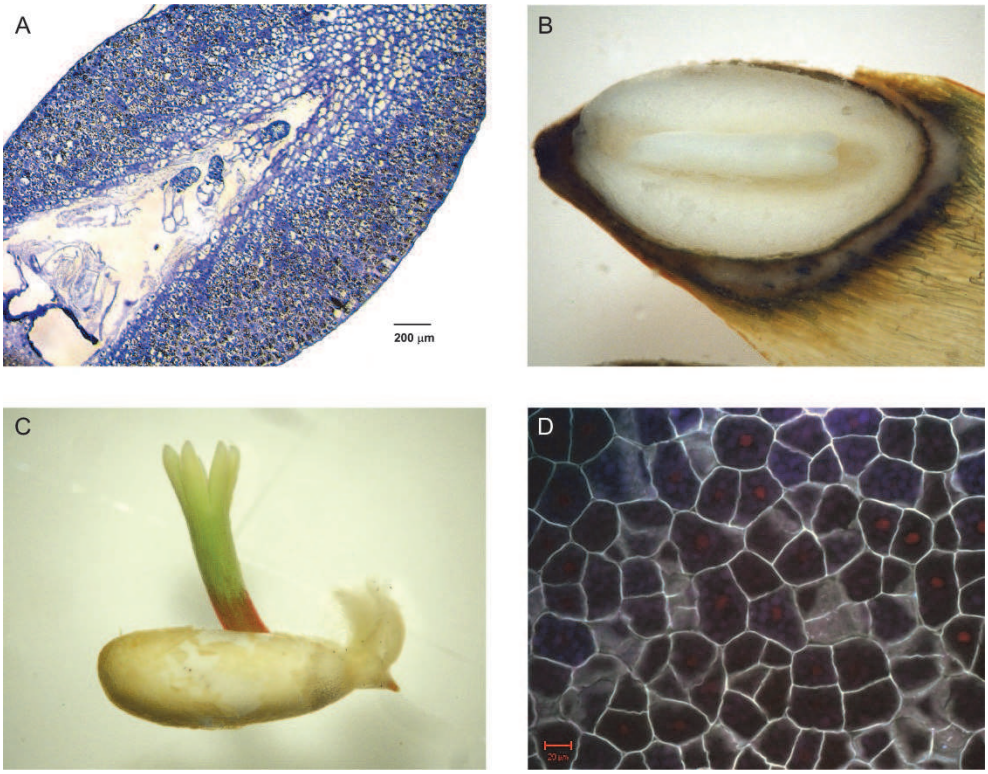

Fig. 1. Scots pine seed development. (A) The dominant embryo and subordinate embryos in the corrosion cavity surrounded by the megagametophyte. (B) A mature Scots pine seed. (C) A young Scots pine seedling. (D) TUNEL positive nuclei in the megagametophyte cells during seed development.

RAD51-like proteins, DMC1, RAD51B, RAD51C, RAD51D, DMC1, XRCC2 and XRCC3 which indicates that Arabidopsis contains the same family of RAD51-like proteins as vertebrates (Klimyuk & Jones, 1997; Doutriaux et al., 1998; Osakabe et al., 2002; Bleuyard et al., 2005). Also, the functions of RAD51 paralogs as well as the different requirements for the RAD51 paralogs in meiosis and DNA repair have been found to be conserved between plants and vertebrates (Bleuyard, et al., 2005). The presence of duplicated intron-free *RAD51* genes in the model moss *Physcomitrella patens* is unique among eukaryotes and may indicate the presence of unusual recombination apparatus in this organism (Markmann-Mulish, 2002). However, NHEJ, rather than HR, has been suggested to be the major pathway for repair DSBs in organisms with complex genomes, including vertebrates and plants (Gorbunova & Levy, 1999). The NHEJ pathway is mediated by KU70-KU80 heterodimer that shows evolutionary conserved functions (Critchlow & Jackson, 1998; Tamura et al., 2002). The KU70 and KU80 proteins of Arabidopsis share about 29% and 23% amino acid sequence identity with human KU70 and KU80 proteins, respectively (Tamura et al., 2002).

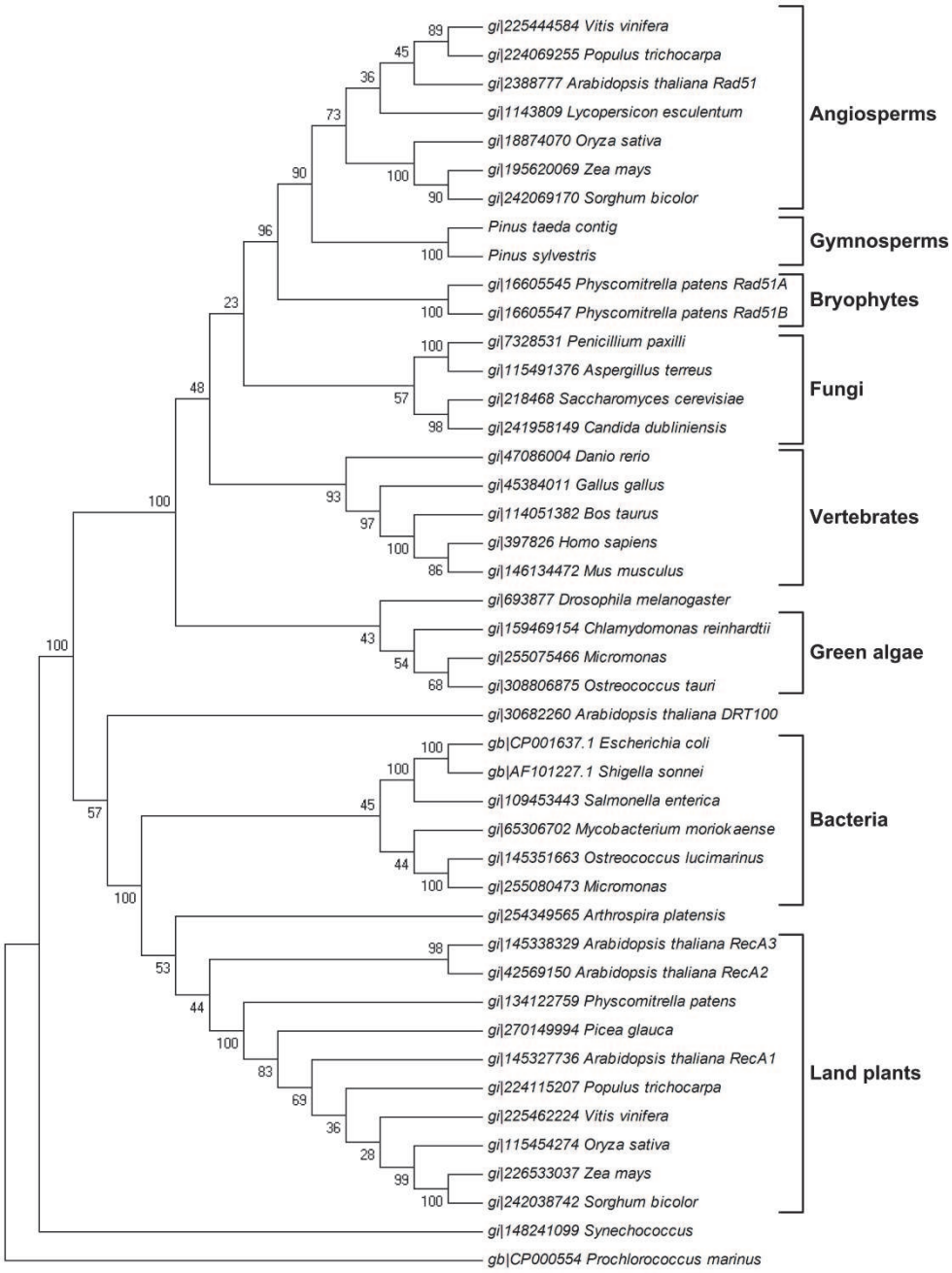

Fig. 2. Phylogenetic analysis of *recA* and *RAD51* sequences.

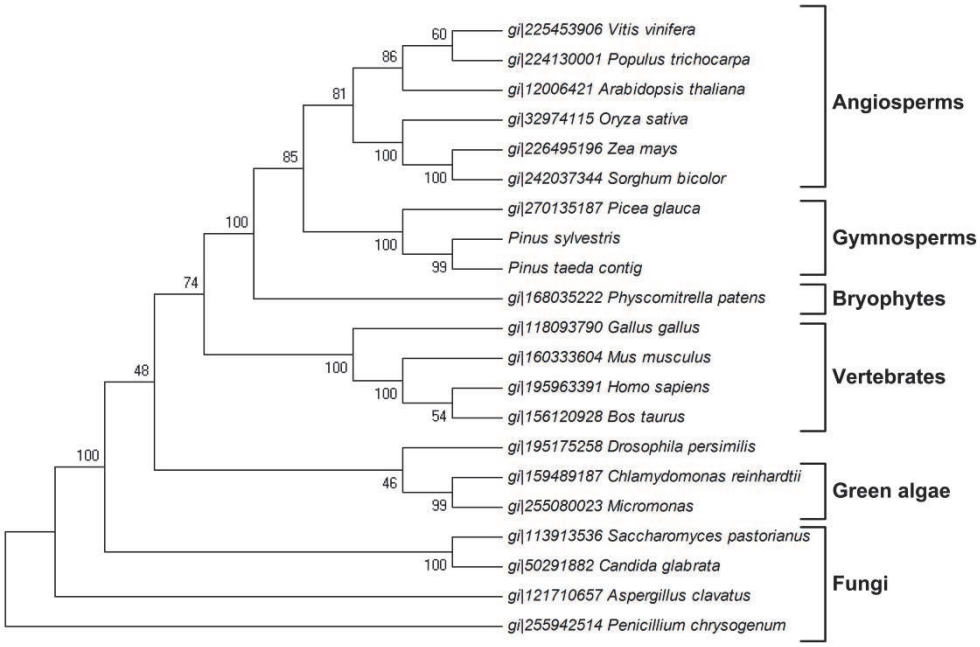

Fig. 3. Phylogenetic analysis of *KU80* sequences.

In the present study, we sequenced the coding regions of the Scots pine putative *RAD51* (GeneBank accession number: JN566226) and *KU80* (GeneBank accession number: JN566225) genes. The predicted amino acid sequences of the Scots pine RAD51 and KU80 proteins showed 77% and 41% identity to the Arabidopsis RAD51 and KU80 proteins, respectively. Blast searches in NCBI databases (http://www.ncbi.nlm.nih.gov) were performed for *recA/RAD51*-like genes as well as for KU80-like genes from various organisms, particularly from the species whose genomes have been completely sequenced. The nucleotide sequences were used for the reconstruction of the evolutionary history of the *recA/RAD51* gene family and *KU80* genes. In the case of other conifers, for which no unigene sequences were available, expressed sequence tag (EST) information was employed to reconstruct a contig containing the complete coding sequence. The nucleotide sequence alignments were performed with ClustalX (Thompson et al. 1997). Phylogenetic analyses were conducted in MEGA4 (Tamura et al. 2007) using the maximum parsimony (MP) method with close-neighbor-interchange algorithm (Nei and Kumar 2000). The bootstrap method (Felsenstein 1985) with 500 replicates was used to evaluate the confidence of the reconstructed trees.

In the phylogenetic tree, *recA* and *RAD51* sequences formed separate branches that were supported by 100% of the bootstraps (Fig. 2). Thus, the result supported the view that eukaryotic *recA* and *RAD51* genes have different evolutionary histories. The phylogenetic analysis suggested a common eukaryotic ancestor for *RAD51* genes, whereas eukaryotes seem to have acquired *recA* genes through horizontal gene transfer from bacteria. Endosymbiotic transfer of *recA* genes may have occurred from mitochondria and chloroplasts to nuclear genomes of ancestral eukaryotes (Lin et al., 2006). Both *RAD51* and *KU80* sequence-based phylogenies (Fig. 2 and 3) were in accordance with the current view

of the evolution of green plants (Qiu and Palmer 1999). That is, morphologically simple plants such as *Physcomitrella* are followed by more complex flowering forms with highly developed breeding mechanisms at the top of the plant phylogeny tree. The novel gymnosperm sequences between bryophytes and angiosperms form the link that has been missing until now in the DNA repair genes based phylogenies.

7. Conclusions

Plants are sessile organisms, which are continuously exposed to a wide variety of biotic, abiotic or developmental stresses, which can cause DNA damages directly or indirectly via generation of ROS. In pines, the mechanisms maintaining genomic integrity must be efficient because the observed mutation rates in somatic cells are not high despite the long lifetime of the organisms. In pines, seed development includes developmentally programmed stresses as well as the strictly co-ordinated action of several cell death programs. Furthermore, pine seed represents an interesting inheritance of seed tissues and anatomically well-described sequences of embryogenesis. Thus, the pine seed provides a favorable model for the study of the effects of a variety of endogenous DNA damaging agents as well as developmentally regulated and environmental stresses on genome integrity. Due to the high evolutionary conservation of the DNA repair mechanisms, the pine seed, as a model system, may also shed light on the mechanisms that contribute to longevity and ageing in eukaryotes in general – things of great interest also with regard to the health of human beings.

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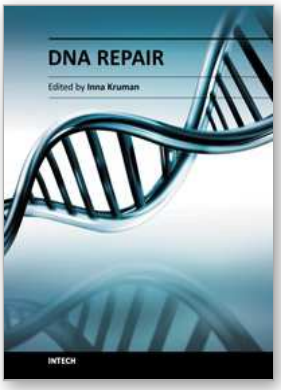

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