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Notes on the poikilochlorophyllous desiccation-tolerant plants

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ABSTRACT   The desiccation-tolerant (DT) plants are poikilohydric and capable of surviving the loss of 90-95% of their cell water content. DT plants are important constituents of many ecosystems from the arctic (lichen and moss vegetations) to the tropics (lichen, moss and flower vegetations). Desiccation-tolerant (DT) plants may be subdivided into homoiochlorophyllous (HDT) and poikilochlorophyllous (PDT) types. The HDTs retain their chlorophyll on desiccation, whereas in PDTs desiccation results in the loss of chlorophyll, which must be resynthetized following remoistening. The PDT strategy can be seen an the evolutionarily different new strategy. It is based on the dismantling of internal chloroplast structure by an ordered deconstruction process during drying, and its resynthesis upon rehydration. The selective advantage of poikilo-chlorophylly is in minimising photo-oxidative damage and not having to maintain an intact photosynthetic system through long (5-10 months) inactive periods of desiccation. Taxonomically the PDT plants appear to be restricted to the monocots. The HDT and PDT strategies solve the same ecological problem, but cover a broad temporal range of adaptation

Acta Biol Szeged 52(1):111-113 (2008)

KEY WORDS

poikilohydry
inselberg
tropical/subtropical
poikilochlorophyllous
homoiochlorophyllous
desiccoplast

Desiccation-tolerant plants can survive the loss of 80–95% of their cell water, so that the plants appear completely dry and no liquid phase remains in their cells; after a shorter or longer period in the desiccated state, they revive and resume normal metabolism when they are remoistened (Tuba et al. 1998). This is a qualitatively different phenomenon from drought tolerance as ordinarily understood in vascular-plant physiology; indeed desiccation tolerance could be seen as a drought-avoiding mechanism in the sense of Levitt (1972). Desiccation tolerance occurs widely in the plant kingdom. It is commonplace among bryophytes and lichens, and is found sporadically among vascular plants of diverse taxonomic affinities.

Desiccation-tolerant (DT) plants may be subdivided into homoiochlorophyllous (HDT) and poikilochlorophyllous (PDT) types. The HDTs retain their chlorophyll on desiccation, whereas in PDTs desiccation results in the loss of chlorophyll, which must be resynthetized following remoistening (Hambler 1961; Tuba et al. 1998). Much has been published on the photosynthetic responses of HDT plants, especially on the cryptogamic plants (Proctor and Tuba 2002). A good deal of information is available on the tolerance limits of HDT desiccation-tolerant cryptogams and phanerogams (Proctor and Tuba 2002; Georgieva et al. 2005). However, until our recent studies (Csintalan et al. 1996; Tuba et al. 1993a, b, 1994, 1996a) little was known about the ecology, ecophysiology and distribution and abundance of PDT plants.

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The aim of this paper is to briefly outline the essential ecophysiological and ecologiocal features of the PDT strategy and the global significance of the DT plants and their vegetations.

The poikilochlorophyllous desiccation-tolerant plants

The poikilochlorophyllous DT (PDT) species dismantle their photosynthetic apparatus and lose all of their chlorophyll during drying; these must be resynthesised following rehydration (Tuba et al. 1994; Sherwin and Farrant 1996). The phenomenon of loss of chlorophyll during desiccation was first described by Vassiljev (1931) in *Carex physodes* from central Asia; the concept was reintroduced and the term poiikilochlorophylly coined by Hambler (1961), and it was regarded as a special case of certain DT monocotyledonous plants (Hambler 1961; Gaff and Hallam 1974; Hetherington and Smillie 1982; Bewley 1979; Gaff 1977, 1989).

The PDT strategy evolved in plants which are anatomically complex and which include the biggest in size of all DT species, and it can be seen as the evolutionarily different strategy. It is based on the dismantling of internal chloroplast structure by an ordered deconstruction process during drying, and its resynthesis upon rehydration by an ordered reconstruction process. These processes can thus be thought of as not only being superimposed on an existing cellular protection mechanism of vegetative desiccation tolerance (Oliver et al. 2000) but as a distinct new class of DT mechanism, as anew

DT strategy (Tuba et al. 1994). The selective advantage of poikilochlorophylly, in minimising photo-oxidative damage and not having to maintain an intact photosynthetic system through long inactive periods of desiccation, presumably outweighs the disadvantage of slow recovery and the energy costs of reconstruction.

Taxonomically the PDT plants appear to be restricted to the monocots (Gaff, 1977, 1989; Bewley and Krochko 1982). Poikilochlorophylly is currently known in eight genera of four families (Cyperaceae, Liliaceae, Anthericaceae, Poaceae and Velloziaceae). Most occupy the almost soil-less rocky outcrops known as inselbergs, in strongly seasonal subtropical climates (Porembski and Barthlott 2000); the best studied physiologically are the African *Xerophyta scabrida*, *X. viscosa* and *X. humilis* and the Australian *Borya nitida* (see Proctor and Tuba 2002).

Xerophyta scabrida (Pax) Th., Dur. et Schinz, is a member of the family Velloziaceae (Velloziales, related to the Bromeliales). It is a C_3 PDT tropical pseudoshrub, c. 0.4-0.9m in height, with perennial leaves. On the top of cliffs it forms a semi desert-like bush vegetation on rocks with a long dry season of 5-6 months (Pócs 1976).The extent of chlorophyll loss in dicotyledons thus varies from species to species, and may be influenced by environmental factors. By contrast, *Xerophyta scabrida*, a characteristic PDT plant, loses all its chlorophylls and dismantles apparently all of the internal structures of the chloroplast during desiccation (Tuba et al. 1993a, b).

Desiccation-induced breakdown of the photosynthetic apparatus in PDT plants is different from the processes involved in leaf senescence. The dismantling of the photosynthetic apparatus can be seen as a strictly organized protective mechanism, rather than 'damage' to be repaired after rehydration. If the PDT plants are desiccated rapidly, they do not have the time to break down chlorophyll and loses viability. *Xerophyta scabrida* preserves most of its chlorophyll when desiccated in the dark, so most the loss seems to be due to photooxidation under natural circumstances (Tuba et al. 1997). This suggests that PDT plants in general probably do not decompose their chlorophyll enzymatically, but rather do not invest in preserving it through the dry state. Dismantling of the thylakoid membranes leads to the formation of nearly isodiametric 'desiccoplasts', which, unlike chromoplasts, are able to regreen and photosynthesise after rehydration (Tuba et al. 1993b). Desiccoplasts contain granular stroma, a couple of translucent plastoglobuli possibly containing lipoquinones and neutral lipids. The thylakoid material is not arranged in plastoglobuli but can be found as osmiophilic lipid material stretched in the place of the former thylakoids (Tuba et al. 1993b). In *X. villosa* not only chloroplast internal membranes but even most of the mitochondrial cristae disappear on dehydration and the remaining ones appear to decompose within 30 minutes after rewetting. This is mirrored by a loss in insoluble or structural proteins (almost 50%), which is much less marked (generally ~10%) in HDT plants (Gaff and Hallam 1974).

On re-wetting *X. scabrida*, reconstruction of thylakoids has already begun by the time the tissue of has reached full saturation. Chlorophyll synthesis starts 8-10 h after rehydration (Tuba et al. 1993a). In this process, osmiophil lipid material is used up. Primary thylakoids with a small stacking ratio make up an intermediate step in resynthesis. Regeneration of the photosynthetic apparatus is complete within 72 hours after rewetting. The restitution of cristae in mitochondria was faster than that of chloroplast internal membranes. Net CO_2 assimilation was first measurable after 24 hours' rehydration. At this point, chlorophyll content was just 35% of that in fully active control plants (Tuba et al. 1993b).

CO_2 gas-exchange of desiccating *Xerophyta scabrida* leaves was studied by Tuba et al. (1996, 1997). Photosynthetic activity declined steeply to zero through the first four days of drying. By this time the leaves had lost about 60% of their water content. The fall in net CO_2 assimilation was caused mainly by the rapid stomatal closure, but it was the decrease in chlorophyll content (as shown by the fluorescence signal) that finally brought photosynthesis to a halt. Dark respiration continued until the 14th day of dehydration, at 24% of the original water content. The declines in water content and respiration were closely correlated. The prolonged respiration during desiccation – termed as desiccation respiration (Tuba et al. 1997) - may cover the energy demand of controlled disassembly of the internal membrane structures in PDT plants (Tuba et al. 1997). In rehydrating *Xerophyta scabrida* leaves, respiratory processes are fully operational before full turgor is achieved (Tuba et al. 1994); fast recovery of respiration is important as the only ATP-source during the primary phase of rehydration (Gaff 1989). A high initial respiration rate on re-moistening, so called 'resaturation respiration' (Smith and Molesworth 1973), is seen in lichens, bryophytes and HDT vascular plants, but this elevated rate persists much longer in PDT species – 30 h in the case of *X. scabrida* (Tuba et al. 1994).

PDT flower species do exist almost exclusively on the tropical/subtropical inselbergs. In these habitats the PDT plants cover globally significant areas with globally significant biomass (our unpublished data). But the DT plants do have a direct practical significance, also: the understanding of mechanisms of DT will be useful in the future to modify species by the powerful technique of genetic engineering, to develop crops that are tolerant of the harmful effects of drought.

Remarks on the ecological role of DT strategies

DT plants are not simply an odd sideline from mainstream homoiohydry (Proctor and Tuba 2002). They are an adaptive optimum in particular ecological situations, and (like 'normal' vascular plants) can be understood fully only in the context

of a wide and multidimensional field of physiological and ecological possibilities.

The HDT and PDT strategies solve the same ecological problem, but cover a broad temporal range of adaptation (Tuba et al. 1998). The HDT pteridophytes and angiosperms are generally adapted to longer drying–wetting cycles than bryophytes and lichens, but to more rapid alternations of wet and dry periods than the PDT monocot species (Schwab et al. 1989; Ingram and Bartels 1996; Sherwin and Farrant 1996; Tuba et al. 1998; Georgieva et al. 2005), though some can survive dry for very long periods of time. The PDT strategy has evolved in habitats where the plants remain in the desiccated state for 5–8(–10) months. Under these conditions it is evidently more advantageous to dismantle the whole photosynthetic apparatus and reconstitute it after rehydration. Of course there is variation within each category and the categories overlap in their ecological adaptation, and two or more may coexist in one habitat, e.g. on inselbergs (Ibisch et al. 1995). Both ends of this ecological spectrum have particular points of interest. There is probably a trade-off between the 'cost' of protection and repair to the photosynthetic apparatus if this is kept in a quickly recoverable state through prolonged periods of desiccation, and the 'cost' of reconstituting the photosynthetic apparatus de novo (Tuba et al. 1998).

The selective advantage of poikilochlorophylly, in minimising photo-oxidative damage and not having to maintain an intact photosynthetic apparatus through long periods of desiccation, presumably outweighs the disadvantage of slow recovery (Tuba et al. 1998). It is more accurate to describe the specific loss of plastid structure during desiccation and its re-synthesis upon rehydration as an ordered deconstruction and reconstruction process (Oliver et al. 2000). This process can then be thought of as being superimposed on an existing cellular protection mechanism of vegetative desiccation-tolerance.

Acknowledgements

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