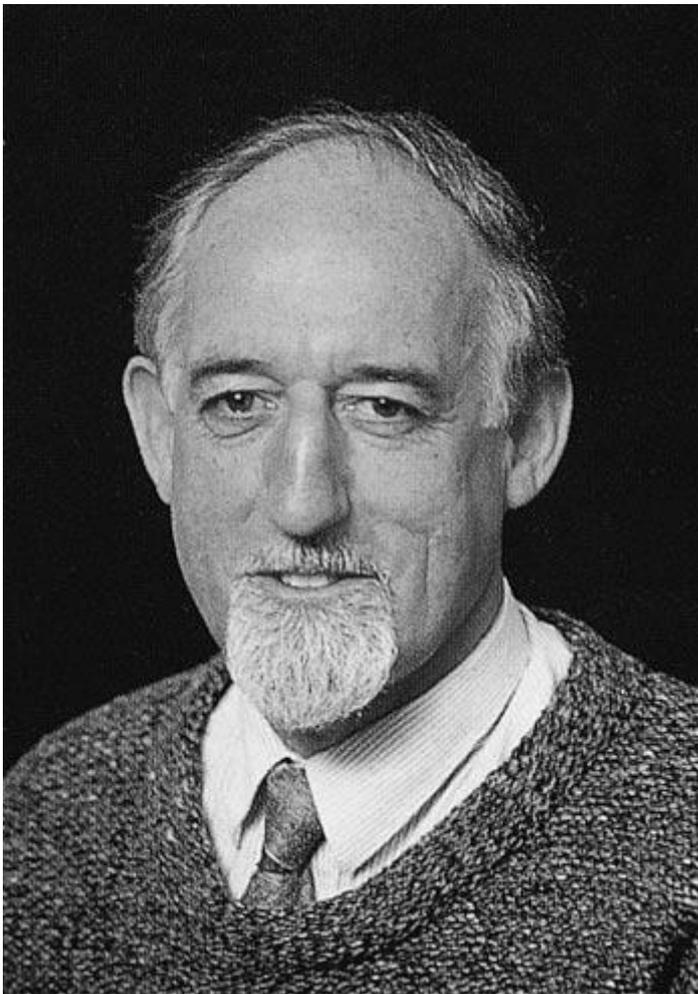


## FEATURE ESSAY 15.1? Resurrection plants

*Don Gaff*



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**Figure 1** Dr Don F. Gaff, Reader at Monash University and foundation member of the Australian Society of Plant Physiologist, has had an enduring interest in drought resistance. Professional experiences now qualify him as a 'plant' revivalist! (Photograph courtesy Bruce Fuhrer, Department of Biological Sciences, Monash University)



[2]

**Figure 2** *Boea hygroskopica* in desiccated condition (lower right) and in fully hydrated form (leafy specimen). Rehydration and restoration of physiological function occurs within a day. Originally described by Ferdinand von Mueller in 1863-64, this specimen was collected at Ravenshoe in North Queensland. Scale bar = 25 mm. (Photograph courtesy Bruce Fuhrer, Department of Biological Sciences, Monash University).

Imagine a leaf shrivelled to a hard dry mass that can rehydrate in 12 to 24 h to resume the crisp texture and vital green colour of a fully functional leaf. Realise, too, that the term ‘dry’ means literally as dry as straw, and is not mere hyperbole. Such a transformation is shown for *Boea hygroskopica* in Figure 2 where a desiccated specimen (lower right) has been superimposed on a subsequently hydrated one.

This inconspicuous but remarkable little plant (Figure 2) was collected at Ravenshoe in North Queensland from a crevice in a basalt bank adjacent to a waterfall. Subjected to spray, such plants remain hydrated but undergo desiccation during dry seasons. They become resurrected the following wet season. As the term implies, such plants are ‘resurrected’ from a dry and seemingly lifeless object to a fully competent organism capable of respiration, photosynthesis and reproductive development! We accept as commonplace the latent life of a dry seed, but such resilience in foliage and growing points seems incredible.

My professional life has centred on plant water relations, and I first became aware of desiccation-tolerant higher plants through Gesner’s 1956 review of poikilohydrous plants in the *Encyclopedia of Plant Physiology*. However, a real appreciation of stress endurance did not come until I had measured the water potential of air-dry leaves of *Myrothamnus flabellifolia* collected in the field in South Africa (-152 MPa), and dried them over concentrated sulphuric acid for several weeks!

Considering that crop plants commonly wilt at a leaf water potential of around only -1.5 MPa, and generally fail to survive reduction in relative water content to values below *c.* 30%, *M. flabellifolia* is a truly remarkable organism.

Recorded discovery of desiccation tolerance in Australia probably dates back to Ferdinand von Mueller’s original 1863–64 description of *Boea hygroskopica* (Gesneriaceae) (Figure 2) which was

collected near Cairns in North Queensland. Although he gave no reason for his choice, the name implies an awareness of its ability to recover from dehydration, a feature demonstrated by the same species shown here. *B. hygroskopica* remains the only dicotyledonous resurrection plant reported from Australia, although a list of 24 monocotyledons and desiccation-tolerant fern species was published in 1978. Four resurrection ferns, for example *Ctenopteris heterophylla*, occur even in moister New Zealand climates; perhaps more will be found in the drought-susceptible niches occupied by epiphytes and lithophytes. However, I went on from early endeavours with *M. flabellifolia* to discover 30 new examples of resurrection species in southern Africa, thus demonstrating that this phenomenon was not as rare among angiosperm plants as originally thought.

Resurrection plants are wonderful examples of biological adaptation to environmental adversity. Most attain the ultimate theoretical limit of protoplasmic drought tolerance: they lose all of their diffusible water and yet survive. They also reflect a rich diversity within our biosphere. Their leaves range from the hard sharp ?bre-packed needles of *Borya* spp. (true xeromorphs), through the broad soft oval leaves of *Boea hygroskopica* (a mesomorph of tropical Queensland), to the soft aerenchymatous leaves of *Chamaegigas intrepidus*, a succulent hygrophyte in the ephemeral pools on granitic hills of Namibia.

Different species of resurrection plants are members of diverse and often unrelated families, suggesting that this feature of desiccation tolerance has evolved on a number of separate occasions throughout evolutionary history. Such con-vergent evolution of physiological properties is also seen in mangroves where different variants of that particular life form occur across a wide range of unrelated families (see Case study 17.1).

Resurrection plants provide us with a window on another aspect of biology. Evolution eventually explores most conceivable adaptations to meet environmental challenges. This occurs either gradually or via sudden changes following hybridisation between species or evolutionary incorporation of endosymbionts into host organisms. In all of these cases genetic adaptations can only step from where they stand initially. Put another way, structures and mechanisms already possessed by an organism (or its symbionts), albeit for un-related functions, will be modified during evolution, rather than a (complex) system arise *de novo*. By implication, the relatively rare desiccation tolerance of resurrection plant foliage has probably evolved from mechanisms of desiccation tolerance already present in pollen and seeds of spermatophytes.

Desiccation tolerance in foliage appears highly complex because the presumed shift from reproductive to vegetative plant structures has only occurred in four monocotyledonous and ?ve dicotyledonous families. Complexity is also implied by the large number of novel proteins synthesised in resurrection plant leaves as moderate drought stress induces tolerance. Significantly, desiccation tolerance is not constitutive in vegetative tissues of resurrection plants but needs to be induced during drying. Here they display dramatically in extent and speed the hardening or acclimation to environmental stress seen in many plant species. During this process, moderate stress induces plants to improve their tolerance limits. They can then survive levels of stress well beyond the stress experienced during hardening, an interesting case of a feed-forward response to deleterious conditions. A resurrection plant progresses from protoplasmic drought-tolerance limits typical of a crop plant to complete desiccation tolerance in only two days!

Once through the zone of potentially injurious low water contents, resurrection plants enter an anabiotic state, which is surprisingly stable; air-dry leaves survive months, even years. In their anabiotic state, leaves of resurrection plants can tolerate temperature extremes from 60°C (short periods) down to snap freezing in liquid nitrogen. In these respects, they resemble dry seed.

Sugars, particularly trehalose, are considered to be able to protect cell membranes and proteins during cell dehydration. Analyses of leaf extracts indicated that trehalose was present in small amounts in all

seven desiccation-tolerant plant species investigated, both in hydrated and dry leaves. The occurrence of trehalose is noteworthy, since trehalose is an unusual sugar in plants. Sucrose contents increased dramatically during drying to become the main sugar, so would appear to be the main protectant, with trehalose and raffinose acting synergistically with sucrose.

Can we harness the desiccation tolerance of resurrection plants for our use? Studies are in progress around the world to identify which genes regulate the phenomenon. A set of 'implementer' genes, expressed in the late phases of drying, appears to protect metabolic systems against dehydration. Genes expressed in earlier phases of drying may include 'regulator' genes, which encode proteins used by implementer genes. If this interpretation is correct, implementer genes probably represent the basis for tolerance shared with seed, whereas their control by specific regulator genes has evolved more recently, and allows expression of implementer genes in vegetative tissue. Addressing this issue, the Monash University group found that over 20 genes were expressed in greater abundance in the resurrection grass *Sporobolus stap?anus* when drought stress stimulated induction of desiccation tolerance in its leaves. The phytohormone abscisic acid (ABA) accumulates dramatically in drought-stressed plants, including all the resurrection plants examined to date. Moreover, exogenous ABA induces desiccation tolerance in two resurrection plants, *Borya constricta* and *Craterostigma plantagineum*. Many of the genes whose expression is enhanced by drought stress in *S. stap?anus* are also upregulated by ABA treatment (Section 10.3.4).

Conceivably, ABA is an important mediator between drought stress and gene activation for desiccation-tolerance mechanisms. However, not all genes that are correlated with induction of desiccation tolerance are responsive to ABA treatment, and by implication a non-ABA pathway for the transduction of the drought stimulus must be involved for desiccation tolerance in *S. stap?anus*. Indeed, four *S. stap?anus* genes are particularly well correlated with desiccation tolerance. Characterisation of these genes and of their regulatory mechanism may well enable transformation of economically important crop and pasture plants so that they can elicit in their foliage the full desiccation tolerance that they already have in their seeds. This has important implications for plant productivity in drought-prone areas and for soil erosion control in dry regions.

## Further reading

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