Commentary

Can water droplets on leaves cause leaf scorch?

There is a widespread belief among both professional and amateur horticulturalists that one should avoid spraying plants during the day, as it is thought by many that the accumulation of droplets on the leaf surface may lead to focusing of solar rays to such an extent that tissue damage (sunburn or scorching) can occur. Considering how widely held this view is, it seems surprising that there appear to have been no rigorous theoretical or experimental analyses of the effect. In this issue of *New Phytologist*, Egri *et al.* (pp. 979–987) at Eötvös University, Budapest, provide what appears to be the first attempt at a rigorous analysis of the optics of sunlit water drops on leaves and the potential effects on leaf 'sunburn'.

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Egri *et al.* analyse the focusing effect of water droplets on different leaf surfaces with differing angles of contact, both theoretically using ray-tracing techniques and experimentally using a limited number of leaf types. In addition, they also use glass beads of different sizes as an alternative experimental system to investigate the potential damaging effects of focused sunlight on leaf tissues. In spite of the widespread nature of the opinion that sunburn can be caused by bright sun when water drops are held on leaves (29 out of the 37 websites these authors found that discuss the topic say that it occurs), Egri *et al.* come to the perhaps surprising conclusion that water drops would only lead to sun scorch in very special circumstances. Egri *et al.* only investigated a small range of leaf types, and in just one environment, so the question remains as to whether they are over-generalizing their results. Damage might be more severe, for example, in very humid environments where evaporative cooling might be less effective, or in other untested species.

Although the glass beads were shown to readily induce sunburn symptoms, sunburn could only be obtained with water droplets where the droplets were held above the leaf surface on hydrophobic hairs, as in *Salvinia*. In other leaves, the focusing effect of the water droplets was inadequate (at least in the plane of the leaf) to cause detectable tissue damage. Egri *et al.* therefore concluded that spraying leaves in bright sunlight would not normally lead to sunburn.

These observations raise a number of interesting questions, of which the following are of particular interest:

(1) Why is it so widely accepted that midday spraying of leaves is damaging when this paper and common sense might suggest that exposure to strong sunlight when there are drops of water on the leaf surface (e.g. after rainstorms) should be a fairly common occurrence, yet plants manage to survive well in most natural environments without obvious leaf damage?

(2) What might the mechanism be of any putative damage?

Why is the recommendation to avoid spraying in sunlight so widely made?

As with many 'old wives' tales', I suspect that there must be some supporting evidence for the belief that one should not water (spay crops) in the midday sun. If such evidence exists, however, it does not appear to have stood the test of peer review, as we cannot find anything in the refereed literature. Perhaps, as suggested by Egri *et al.*, the reason to avoid watering during bright sunlight has much more to do with considerations other than tissue damage, such as the lower effectiveness of water applied during the day than during the night (with more evaporating directly rather than wetting the soil). A possible reason for the perception that spraying leaves in bright sunlight causes damage may in fact result from the common occurrence of white spots on leaves caused by precipitation of dissolved salts after spraying with impure water (e.g. when using pesticide or water with high ionic content – see Fig. 1).

Although one instinctively feels that the vast body of 'old wives' cannot all be wrong, it is interesting to remark in passing that general beliefs are often strongly held in spite of the absence of supporting evidence. Indeed there are many other phenomena that are widely accepted even though conventional scientific studies can find no scientific basis for them; a well-known example is homeopathy (Goldacre, 2009).

Fig. 1 Photograph of a seedling leaf on a *Lactuca serriola* L. plant after exposure to bright sun for *c.* 1 h at midday in Canberra (Australia) with a drop of pond water on the leaf at the position where the white mark is observed. Another, recently applied droplet is also shown. The white mark could be easily removed by rubbing the leaf, suggesting that it was a superficial deposit.

My own suspicion is that the main reason for the opinion that spraying water on leaves during sunny periods can lead to damage arises from the precipitation of salts as water dries (Fig. 1). Perhaps this paper will stimulate the documenting of real cases of sunburn from raindrops. The Egri *et al.* paper provides a good illustration of the need to fully check 'well known' phenomena or 'factoids' to confirm their truth, although, as with any scientific study, it is always difficult to prove the negative (lack of an effect) and I still consider that the authors' conclusions need to be tested for a much wider range of conditions and species. Indeed I feel that they perhaps go too far when they state that 'water drops cannot cause sunburn, either on water-repellent or on wettable leaves with smooth, hairless surfaces'. At least in the case of sunburn in leaves there is a rational basis for the belief in possible damage with some clear mechanistic hypotheses (see following section).

A mechanism for any damage?

Egri *et al.* assume that damage is caused by high temperatures resulting from the elevated irradiance near the optical focus, although they provide no direct evidence to support this assumption, other than the circumstantial comparison between the effects of glass beads (where there is no evaporative cooling effect), and the results with *Salvinia* leaves where the water drop does not contact the leaf lamina. The increase in irradiance (over limited areas) at the level of the leaf with droplets is not as great as with a truly spherical glass bead, partly because of the imperfect focusing into an extended caustic. Although Egri *et al.* show that light enhancement above the value found with no drops on the leaf can be up to 175-fold for a hemispherical drop on a plane (*Platanus hybrida*) leaf, in most cases the enhancement is much smaller. Because such an enhancement must be spread over a very small area (1/175 of the area of the collecting drop) one would not expect this to lead to thermal stress because of the capacity for lateral heat transfer within the leaf (Jones, 1999), the thermal damping provided by the large thermal mass of the water drop, and the cooling effect of evaporation from the drop. Where the focal point lies outside the footprint of the drop, however, the latter two processes might be expected to make only a small contribution to protection of the leaf from thermal damage. On the other hand, one might expect substantial photoinhibitory damage (Demmig-Adams *et al.*, 2006) to the photosystems if the focusing should continue beyond very brief periods (but, of course, the solar angle changes continuously so any one part of the tissue would only be briefly exposed to such intense irradiation).

It would be interesting to test whether photoinhibitory damage occurs in such a system. This could be investigated, for example, by using chlorophyll fluorescence imaging (Baker, 2008). Interestingly Pearcy (1990) found no clear evidence for photoinhibitory damage caused by natural sunflecks in plant canopies (where irradiances may be well over one order of magnitude greater than the normal illumination), although regulatory processes such as down-regulation through, for example, the xanthophyll cycle occurred in several cases. The much higher intensities potentially found in the areas of focus under water drops might conceivably lead to damage and photobleaching, but again I know of no evidence to support this hypothesis.

Conclusions

Egri *et al.* do not speculate in detail about the putative mechanisms for tissue damage, but the implication seems to be that any damage (as occurred with the *Salvinia* leaves) is primarily a result of high temperature. A better understanding of the phenomenon would require further information on both the temperature threshold that would need to be exceeded for burning or scorching to occur and on the potential for enhanced irradiances in small areas to affect local tissue temperatures. One might also speculate that an alternative phenomenon could be photodamage to the photosystems in the chloroplasts, but again we have little information about the prevalence of such a phenomenon.

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Key words: hydrophobic hairs, leaf tissue, optical focus, photoinhibitory damage, sun or scorch burn, water droplets.

Dandelions 'remember' stress: heritable stress-induced methylation patterns in asexual dandelions

Plants exhibit a variety of genetic and epigenetic responses to environmental stresses. A well-known response is that transposable elements can be activated (reviewed in Wessler, 1996); other common responses include changes in gene expression levels and patterns (e.g. Kilian *et al.*, 2007), as well as changes in alternative splicing patterns (e.g. Palusa *et al.*, 2007). Among epigenetic phenomena, changes in DNA methylation in response to stress have been investigated in several plants, and both increases and decreases in methylation levels have been discovered (reviewed in Bruce *et al.*, 2007; Lukens & Zhan, 2007; Boyko & Kovalchuk, 2008; Chinnusamy & Zhu, 2009). In some cases the altered methylation levels did not change back to the original levels after the stress was removed (e.g. Steward *et al.*, 2002). In this issue of *New Phytologist*, Verhoeven *et al.* (pp. 1108–1118) now show that cytosine methylation patterns in asexual triploid dandelions can change at some loci in response to stress conditions. Moreover, and most notably, some of the altered methylation patterns were heritable in the next generation.

> *…most notably, some of the altered [stress induced] methylation patterns were heritable in the next generation.'*

In their study, Verhoeven *et al.* used asexual, or apomictic, triploid dandelions that reproduce with unfertilized seeds, thus minimizing or eliminating genetic variation among individuals. They used eight plants in each of four stress treatments plus untreated control plants. The stress conditions included high salt, low nutrients, salicylic acid and jasmonic acid stresses; the latter two were used to induce anti-herbivore and anti-pathogen defenses. Changes in methylation were assayed in each plant using the amplified fragment length polymorphism (AFLP) technique with diagnostic methylation-sensitive and methylation-insensitive restriction enzymes. Twenty out of 359 scorable fragments showed evidence of a change in methylation (either gain or loss of methylation) in one or more treatments and in one or more individuals. A large majority (74–92%) of the altered methylation patterns were transmitted to the progeny of the stressed plants that were not exposed to the stresses. The salicylic acid treatments showed the largest number of heritable methylation changes.

The fascinating results uncovered by Verhoeven *et al.* raise many questions about the phenomenon of heritable stress-induced methylation patterns. It will be particularly interesting and important to determine which types of DNA sequences undergo methylation changes in response to environmental stress that are heritable. Are they coding regions, introns, or regulatory regions of genes? Or are they intergenic regions of the genome? Might many of the methylation changes be in transposable elements? Sequencing of the AFLP fragments that displayed the heritable methylation changes in the study by Verhoeven *et al.* could begin to answer those questions. In addition, the number of methylation changes in a locus could be determined by bisulfite sequencing on some of the loci that were identified by AFLP analysis. In addition, a larger number of loci could be screened by AFLP to identify additional loci that undergo heritable methylation changes in order to shed light on the frequency of different types of DNA sequences involved. If