Dimethylsulphoniopropionate (DMSP) and related compounds in higher plants

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Abstract

Dimethylsulphoniopropionate (DMSP) is produced in high concentrations in many marine algae, but in higher plants only in a few salt marsh grasses of the genus Spartina, in sugar canes (Saccharum spp.), and in the Pacific strand plant Wollastonia biflora (L.) DC. The high concentrations found in higher plants (up to 250 μmol g⁻¹ dry weight) suggest an important role, but though many functions have been suggested (including methylating agent, detoxification of excess sulphur, salt tolerance, and herbivore deterrent), its actual functions remain unclear. The fact that the ability to produce DMSP in high concentrations is found in species that have no taxonomic or ecological relationship suggests that the compound evolved independently and serves different functions in different plants. This is supported by observations that DMSP in W. biflora behaves differently from that in Spartina species. While DMSP concentrations in W. biflora have been found to increase with increasing salinity, suggesting a role in osmotic control, such a relationship has not been found for DMSP in Spartina species. Recent observations on tissue culture showed that, while undifferentiated tissue of W. biflora produced DMSP, such material of Spartina alterniflora Loisel. did not. Ongoing studies with tissue culture of both species have opened up new avenues of research on DMSP in higher plants, ultimately to elucidate the functions of this enigmatic compound.

Key words: Dimethylsulphoniopropionate, Spartina sp., tissue culture, Wollastonia biflora.

Introduction

Dimethylsulphoniopropionate (DMSP) is found in high concentrations in many marine algae (Dickson et al., 1980; Karsten et al., 1990; Kiene et al., 1996; Malin and Kirst, 1997; Stefels, 2000; Van Alstyne et al., 2003). It is much less common in higher plants and in high concentrations it has so far only been identified in three genera: grasses of the genera Spartina (cordgrass) and Saccharum (sugarcane), and in the dicotyledonous strand plant Wollastonia biflora (also known as Wedelia biflora or Melanthera biflora) (Table 1). While most Spartina species and W. biflora naturally occur in saline, often coastal environments, Saccharum spp. do not. Within the genus Spartina, not all species produce the compound. For example, the North American Spartina species S. alterniflora Loisel., S. cynosuroides (L.) Roth, and S. patens (Aiton) Muhl. are often found adjacent to each other in salt marshes along the east coast, but of these three only S. alterniflora produces the compound in high concentrations (Otte and Morris, 1994).

While DMSP has been identified in low concentrations (>1 μmol g⁻¹) in a wide range of plants (Paquet et al., 1994, 1995), so far only the species listed here (Table 1) have been found to produce concentrations of several orders of magnitude higher. Otte and Morris (1994) reported average values of up to 250 μmol g⁻¹ or 3.38% of dry weight in green leaves of S. alterniflora. Up to 86% of the total concentration of S in these plants was allocated to DMSP. This means that these species allocate significant resources to the production of DMSP, but the function(s) of the compound have so far eluded researchers. This paper reviews the authors’ knowledge of DMSP in higher plants and discusses its proposed functions.

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Biosynthesis

All DMSP-producing plants, including algae, synthesize the compound from methionine, but the pathways from methionine to DMSP differ between plant groups and species (Hanson et al., 1994; Stefels, 2000; Kocsis and Hanson, 2000). While in algae, methionine is first transaminated to form 4-methylthio-2-oxobutyrate (MTOB), in higher plants methionine is first methylated to form $S$-methyl methionine (SMM), and the pathway in grasses is different from that in W. biflora. In the light of its possible functions, it may be important to realize that, regardless of the actual pathway, DMSP synthesis is linked to the amino acid pathways, but that DMSP itself does not contain nitrogen (see ‘Overflow for excess reduced compounds or energy or storage of S’ below). Hanson and co-workers located DMSP biosynthesis in W. biflora in the cytosol, with the last step associated with the chloroplasts (Trossat et al., 1996, 1998). It was recently observed that undifferentiated non-photosynthesizing tissue culture (calli) of W. biflora leaves still produced DMSP to concentrations of 15–35 \( \mu \text{mol g}^{-1} \text{FW} \) (Moran, 2001), suggesting that fully developed chloroplasts are not required for the biosynthesis of DMSP. However, preliminary analysis in this laboratory of calli from S. alterniflora could not ascertain the presence of DMSP.

Localization in tissues

Probably because most investigators find that DMSP concentrations are typically higher in the green tissues of plants than in the non-photosynthesizing parts, few studies have addressed the distribution of DMSP within plants. However, that does not mean that DMSP in plant parts other than the leaves is not important. In fact, Mulholland and Otte (2000) provided data to show that DMSP in roots and stems of S. anglica may be much more important than previously thought. These authors showed (Fig. 1) that, although the concentrations in leaves decreased with increasing nitrogen supply, whole plant DMSP content increased.

In addition, the distribution between the plant parts changed; relatively more DMSP was present in the leaves under low nitrogen conditions than under high nitrogen conditions. This, together with the observation that the amount of S allocated to DMSP in the leaves decreases with increasing N-supply (Otte and Morris, 1994), suggests that DMSP is translocated from the leaves to the stems and roots upon increased nitrogen supply.

Proposed functions in higher plants

Precursor of dimethyl sulphide (DMS) and acrylate

One function of DMSP may simply be as a precursor for its degradation products DMS and acrylate (Otte and Morris,
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DMSP is a gas with a strong smell and both compounds are relatively toxic, and so may act as herbivore deterrents (see ‘Herbivore deterrent’ below). Acrylate is also highly reactive and could be rapidly recruited as a source of carbon (see ‘Overflow for excess reduced compounds or energy or storage of S’ below). However, it is difficult to understand why the plants would accumulate such high concentrations of DMSP relative to the low production rate of DMS and acrylate. Otte and Morris (1994) calculated a turnover rate, based on the assumption that the only consumption pathway of DMSP would be through the DMS/acylate degradation pathway, of about 1 per 0.6 years.

Methylation

Challenger and co-workers were the first to isolate DMSP in pure form from marine macro-algae (Challenger and Simpson, 1948) and the compound was implicated in biological transmethylation reactions (Dubnoff and Borsook, 1948; Challenger et al., 1957). However, even though DMSP appeared to be involved in transmethylation reactions in cell-free solutions (Ishida and Kadota, 1968) and in various animals (Ishida, 1996; Nakajima, 1996), this function could not be proven in plants (Ishida, 1996). Weber et al. (1991) too did not find evidence of the involvement of DMSP in the methylation of tin in *S. alterniflora*.

Osmoregulation

Of all the proposed functions, the possible involvement of DMSP in osmoregulation has had by far the most attention. This is partly based on the structural similarity of this tertiary sulphur compound with quaternary ammonium compounds such as glycinebetaine, a known compatible organic solute (Fig. 2), partly due to the fact that, in algae, the compound appears to be found predominantly in marine and estuarine species. There have been several studies on the osmoregulatory function of DMSP in algae (Dickson et al., 1980; Kirst, 1996; Van Bergeijk et al., 2003). ‘Classic’ compatible solutes, such as glycinebetaine and proline, are accumulated to higher concentrations in plants in response to increased exposure to salinity, as has been observed in *S. alterniflora* (Cavalieri and Huang, 1981; Cavaleri, 1983). Indeed, Dacey et al. (1987) observed that concentrations of DMSP appeared to increase in *S. alterniflora* with increasing salinity. However, nitrogen was a co-variant in that study and it was later found that both in algae (Gröne and Kirst, 1992; Stefels, 2000) and *Spartina* species (Otte and Morris, 1994; Colmer et al., 1996; Mulholland and Otte, 2000, 2002) nitrogen supply to the plants strongly affects concentrations of DMSP in the tissues. In fact, Otte and Morris (1994) and Colmer et al. (1996) independently showed that neither salinity nor sulphur supply to *S. alterniflora* affected DMSP concentrations in the plants, but N supply did. DMSP concentrations in leaves decrease with increasing N-supply, and this effect cannot be explained by simple dilution/concentration effects, but is due to a lower net accumulation rate (including translocation to other plant parts, as explained above) of DMSP in plants with a high nitrogen supply (Otte and Morris, 1994).

While there are indications that DMSP may be involved in the osmoregulation of the Pacific strand plant *W. biflora* (Storey et al., 1993), the data for *Spartina* species so far suggest that if it is involved in osmoregulation at all, DMSP does not behave like a classic compatible solute. Greenway and Munns (1980) and Leigh et al. (1981) suggested that compatible organic solutes could be involved in osmoregulation without changes in their concentrations at the tissue level by moving between the cytoplasm and the vacuoles within the cells, depending on the osmotic potential of the cytoplasm. Mulholland (2000) subsequently proposed this as a possible mechanism for the involvement of DMSP in osmoregulation in *Spartina* species (Fig. 3).

In addition, the high concentrations of DMSP in the tissues of *Spartina* spp., *W. biflora*, and *Saccharum* spp. would contribute to a high baseline osmotic potential, thus giving a constitutive tolerance to salinity-related stress (Otte and Morris, 1994; Colmer et al., 1996; Stefels, 2000). Although the origin of sugarcanes is not associated with coastal or marine habitats, DMSP might still be involved in osmoregulation, for example, in response to drought.

Sink for excess S and S-detoxification

In addition to being exposed to varying levels of salinity, the *Spartina* species that produce DMSP in high concentrations tend to live in coastal salt marshes with typically high concentrations of sulphide in the sediments and porewater. Carlson and Forrest (1982) showed that *S. alterniflora* can take up S as sulphide, despite it being potentially toxic at relatively low concentrations in many organisms. It was therefore proposed that DMSP might be involved in sulphide detoxification mechanisms in the plants (Havill et al., 1985; Van Diggelen et al., 1986).
The idea was that excess sulphide would be incorporated into DMSP, which would subsequently be enzymatically degraded to acrylate and the gas DMS. This would thus be a route for the removal of sulphur from the plants. Although Van Diggelen and co-workers observed increased DMSP concentrations in *S. anglica* at the highest exposure levels to sulphide, such a response was not observed for *S. alterniflora* by Otte and Morris (1994). The latter argued that the observations by Van Diggelen and co-workers could be explained by dilution–concentration effects, because increased exposure to sulphide led to reduced growth. In addition, as already mentioned above, it seems that the very low turnover rate of DMSP to DMS would not be sufficient to effectively remove S from the plant tissues.

**Overflow for excess reduced compounds or energy or storage of S**

Stefels (2000) speculated that DMSP may be part of an overflow mechanism to regulate cysteine and methionine levels, when the influx of sulphur exceeds the cell’s conversion capacity into amino acids, proteins, and other sulphur-containing compounds. Excess sulphur would be removed via degradation of DMSP to DMS and acrylate, but it is questionable whether or not this would be a rapid enough process. However, if DMSP could be converted back to methionine, as has been suggested to occur in animals (Dubnoff and Borsook, 1948), this not only would address an imbalance between N and S metabolism, but could also serve as temporary storage of S in a readily available form for fast recruitment back into the S-cycle (Mulholland, 2000). Such a mechanism could also explain observations of negative correlations between concentrations of glycinebetaine and DMSP in *S. anglica* (Mulholland et al., 1997).

**Herbivore deterrent**

DMSP is an analogue of vitamin U, also known as S-methyl-L-methionine (Fig. 2), which stimulates growth in fish. The possible benefits of DMSP to fish and other animals were therefore investigated by Nakajima (1991a, b, 1992, 1996), who found that DMSP (also known as dimethyl-β-propiothetin, DMPT) seemed more beneficial to fish than vitamin U. Earlier the same author (Nakajima, 1989) tried to investigate if DMSP had any effects on rats, only to find that it was difficult to feed DMSP at high concentrations, supposedly because the rats did not like the taste and smell of the compound. Then during the late 1980s and early 1990s, Morris and co-workers observed that *S. alterniflora* plants in a long-term fertilization experiment at Goat Island, North Inlet, South Carolina (Morris et al., 2002; Sundareshwar et al., 2003) that had been fertilized with nitrogen were more frequently attacked by rice rats (*Oryzomys palustris*) compared with plants growing in unfertilized plots. The rice rats would typically eat through the outer sheaths of the stem near the base of the plants in order to reach the young shoots growing inside. This inner tissue only was eaten by the rats. As concentrations of DMSP in *Spartina* decrease upon supply of nitrogen (Otte and Morris, 1994), it was suspected that the plants that were attacked, which were almost solely associated with the N-fertilized plots, contained lower levels of DMSP. Upon analysis it was found that the tissues of plants in fertilized and unfertilized plots were similar, except for the inner tissues of the stems, consisting of the leaf primordia, and that this tissue contained much lower concentrations of DMSP than the same tissue in plants from unfertilized plots (Fig. 4).

These observations suggest that DMSP in *Spartina* could act as a herbivore deterrent. In fact, Van Alstyne et al. (2003), observing that DMSP levels in algae were not very responsive to changes in salinity, argued that the herbivore deterrent function of DMSP was more important than that of osmoregulation. The effect may be directly due to the taste and smell of the compound itself. The accumulation of substantial amounts of DMSP on the leaf surface (Pakulski and Kiene, 1992) may also contribute to this direct effect. In addition, an indirect effect via degradation of DMSP to dimethyl sulphide and acrylate, as has been suggested for algae (Strom et al., 2003; Van Alstyne and Houser, 2003) would also contribute to the herbivore-deterrent properties of the compound.

**Cryoprotectant**

It has been suggested that DMSP has a function in cryoprotection in algae, particularly in polar regions (Karsen et al., 1996). This function has not been investigated in higher plants, but it may explain why *S. alterniflora* and related species are found in colder climates than might be expected. *S. alterniflora* is common along the east coast of North America, forming vast expanses of near monoculture in the south-eastern USA. With *C*₄ characteristics, it would...
be associated more with warm climates, but this species is found as far north as Labrador where winters are extremely cold and ice action is a common feature (Roberts and Robertson, 1986; Adam, 1990).

Antioxidant

Recently, the potential function of DMSP and related compounds as antioxidants in the diatom Thalassiosira pseudonana and the coccolithophore Emiliania huxleyi was investigated (Sunda et al., 2002). This function has not been studied in higher plants. However, although DMSP is certainly able to act as an antioxidant from a chemical point of view, it is difficult to imagine that higher plants such as *S. alterniflora*, which accumulate DMSP to concentrations of more than 3% of dry weight, would have evolved this ability for the sole purpose of that function.

Conclusion

Although not produced in high concentrations in many higher plants, the synthesis of DMSP in plants is not a rare occurrence, and its ecological importance is only now being uncovered. In addition to the functions of the compound (algae compared with higher plants) suggests that the ability to produce DMSP developed several times during the evolution of plants.

DMSP is a compound that clearly deserves attention. Recent improvements in the analysis of DMSP and related compounds, direct analysis by HPLC (Colmer et al., 2000) instead of indirect head-space GC analysis via DMS from DMSP upon alkaline hydrolysis (Otte and Morris, 1994), have greatly improved the ability to quantify and identify these compounds in plant tissues. Another promising development is the establishment of tissue cultures of DMSP-producing plants (Moran, 2001), which has opened up new approaches to research at the cell level of higher plants, and thus provides another avenue towards understanding the functions of DMSP.

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