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The potential of smoke in seed technology

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Smoke is an important factor involved in fire and post-fire germination cues. The role of smoke in stimulating germination was first highlighted in South Africa in a study on *Audouinia capitata*, a threatened fynbos species. Further studies on South African fynbos, Californian chaparral and Australian species have illustrated the widespread ability of smoke to promote germination of many species from fire-prone areas. However, smoke-stimulated germination is not limited to species from fire-prone habitats, and a variety of species from fire-free habitats also respond positively. Smoke and aqueous smoke extracts can potentially be used for a variety of applications related to seed technology. These include uses in horticulture, agriculture, ecological management and rehabilitation of disturbed areas.

Introduction

Many species of fynbos, the dominant vegetation type in the Cape Floristic Region, are dependent on fire to provide suitable germination cues. Other similar ecosystems, such as chaparral (southern California), kwongan (Australia) and areas of the Mediterranean also show similar requirements for fire-related cues to stimulate the seed germination of many species. The effect of fire on seed germination from areas where wildfires form an integral part of the ecology is well documented (Fenner 1995, Keeley and Fotheringham 2000, Probert 2000). The stimulatory effect of fire may result from a number of different effects, including the physical one of dry heat on seed coat structure, the physiological effect of dry heat on seed embryos, and/or the dormancy-breaking effects of volatile compounds such as ethylene and ammonia (Van Staden *et al.* 1995a, Keeley and Fotheringham 2000).

In addition, plant-derived smoke plays an important role in breaking the dormancy of many species. De Lange and Boucher (1990) were the first to demonstrate that smoke, and aqueous extracts of smoke, was responsible for the stimulation of seed germination of a threatened fynbos species, *Audouinia capitata*. Following this significant discovery Brown (1993a, 1993b) showed that other fynbos species, from several genera and families, also exhibited improved germination with smoke treatments.

Surveys, mainly focused on species from fire-prone areas, have shown that smoke is effective on species from a wide range of families, which vary in ecology, reproductive strategy, seed size and morphology (Brown *et al.* 1993a, Dixon and Roche 1995, Pierce *et al.* 1995, Roche *et al.* 1997a, Van Staden *et al.* 2000). However, the promotion of germination by smoke is not limited to species from fire-prone habitats. For example, germination can also be stimulated in lettuce (Drewes *et al.* 1995), celery (Thomas and Van Staden 1995), red rice (Doherty and Cohn 2000) and one species of wild oat (Adkins *et al.* 2000).

Although there has been a continued effort to elucidate the active principle(s) in smoke, the identity of the chemical component(s) and the physiological mechanisms of action remain unknown (Baldwin *et al.* 1994, Van Staden *et al.* 2000, Keeley and Fotheringham 2000). Keeley and Fotheringham (1998a, 1998b, 2000) have concluded that the most likely active component is nitrogen oxide. However, Doherty and Cohn (2000), in a study of red rice, found that liquid smoke extracts lacking nitrogen oxides also elicited a positive germination response. In another study, the nitric oxide scavenger carboxy-PTIO did not inhibit the smoke-stimulated germination of Grand Rapids lettuce seeds (Light and Van Staden 2003).

Despite the fact that the identity of the active compound(s) and the mode of action are unknown, the remarkable effects of smoke and aqueous smoke extracts are well known and utilised for their effect on seed germination. For example, recent studies by Lloyd *et al.* (2000), Read *et al.* (2000), Rokich *et al.* (2002) and Tang *et al.* (2003) have used smoke to investigate the size and spatial extent of soil seed banks.

Although the role of smoke as a germination cue has been previously reviewed (Brown and Van Staden 1997, Van Staden *et al.* 2000, Minorsky 2002), the aim of this paper is to highlight the recent findings related to smoke stimulated germination (2000–2003). More particularly, however, this paper also aims to focus on the application of smoke technology, and the potential which exists for the use of smoke in horticulture and agriculture.

Horticulture

In recent years 'indigenous gardening' has become more popular in South Africa. Unfortunately, many fynbos species are difficult to germinate and cannot easily be propagated by the public. The use of smoke technology, however, can be used to promote the germination of many of these plants for garden use and sale to the public. Brown and Botha (2002) have recently published an updated list of the fynbos species which have seeds that exhibit a good germination response to smoke. The seeds of more than 300 fynbos species have been tested for a germination response to smoke or aqueous smoke extracts. Of these, 157 species have shown a positive response and include members of the Asteraceae, Bruniaceae, Campanulaceae, Caryophyllaceae, Crassulaceae, Ericaceae, Fabaceae, Geraniaceae, Haemodoraceae, Iridaceae, Mesembryanthemaceae, Molluginaceae, Penaeaceae, Poaceae, Polygalaceae, Proteaceae, Restionaceae, Rosaceae, Rutaceae, Scrophulariaceae, Stilbaceae and Thymelaeaceae.

Of particular importance has been the dormancy breaking of many of the Restionaceae species (Cape reeds). These important fynbos species have great potential for landscaping and for the wildflower trade. Prior to the use of smoke for promoting seed germination, many of the approximately 300 species were difficult or impossible to propagate from seed. However, many of these species respond well to smoke treatments and are now available more easily for horticultural use (Brown *et al*. 1994, Jamieson and Brown 1995). The use of smoke in propagating other horticulturally important plants, such as *Syncarpha vestita* (Cape everlasting), is also important as it can allow for cultivation of these species thereby reducing the pressure on wild populations as a result of collecting (Brown *et al*. 1993b).

The retention of the germination cue, once seeds have been exposed to smoke, allows for the pre-treatment and subsequent storage of seeds prior to sowing (Baxter and Van Staden 1994, Brown *et al.* 1998, Brown and Van Staden 1999, Tieu *et al.* 1999). The ability of the smoke cue to be retained during storage has important implications for a number of applications. Seeds can be pre-treated with smoke for use in horticulture, agriculture and in ecological rehabilitation.

Researchers at Kirstenbosch Botanical Gardens have developed a seed primer which incorporates aqueous smoke extracts and a mixture of other natural germination stimulators. The dehydrated seed primer is impregnated on to absorbent paper which can be used by gardeners. The product is marketed as 'Kirstenbosch Instant Smoke Plus Seed Primer' (Brown 1994).

In Australia, researchers at King's Park and Botanic Gardens have contributed significantly to investigating the effect of smoke-stimulated seed germination (Dixon *et al.* 1995, Roche *et al.* 1997a). The germination enhancement of Australian species by smoke has been reported in more than 170 species from 37 families (Roche *et al.* 1997a, Bell 1999). They have also developed a similar commercial product which is marketed as 'Seed Starter'. It is a concentrated smoke solution which is used in a diluted form.

Agriculture

Some vegetable crops, such as lettuce (Drewes *et al.* 1995) and celery (Thomas and Van Staden 1995), have shown enhanced germination with smoke. Smoke treatments could possibly be used to promote synchronous germination of seeds, and to increase the rate of germination of certain agricultural crops. As mentioned earlier, seeds can be successfully pre-treated with smoke. This is an aspect of smoke-stimulated seed germination which has not been fully explored, although it is potentially very useful.

A recent study by Modi (2002) has investigated the indigenous storage method of maize in South Africa. Traditionally, rural subsistence farmers store their maize cobs (containing seeds) over a fireplace in a hut. This indigenous method of maize storage thus causes the seeds to come into contact with large quantities of smoke. The study conducted by Modi (2002), using two traditional maize landraces, showed that the seeds exposed to smoke had a higher germination rate and final germination than untreated seeds (see Modi, this issue). Furthermore, smoke-treated seeds produced significantly more vigorous seedlings (heavier and taller) than untreated seeds.

Weed Control

Many weed species have the ability to persist in the soil seed bank for several years due to seed dormancy. This attribute often hampers the task of predicting the timing and the extent of weed emergence, for weed management in agricultural systems (Adkins *et al.* 2000, Benech-Arnold *et al.* 2000). Since many weed species respond favourably to smoke treatments, it is possible to evaluate the extent to which a soil seed bank is contaminated by weed seeds, and also assess the seed reserve of indigenous species (Van Staden *et al.* 2000).

It may be possible to use smoke technology to manage weed populations of arable land by breaking dormancy to maximise seedling emergence, and then using other mechanisms for weed eradication (Benech-Arnold *et al*. 2000). Smoke technology may be used in agricultural management to reduce the weed burden on crops and decrease the need for herbicides or physical weed control. Furthermore, it may even be possible to deplete arable weed seed banks through appropriate smoke treatments (Adkins *et al.* 2000, Adkins and Peters 2001). However, this aspect of smoke stimulated seed germination of weedy species requires more research, particularly in agricultural ecosystems.

Habitat Restoration

In the Western Cape Province of South Africa, programmes are in place to remove dense stands of invasive alien trees and shrubs that threaten the fynbos vegetation and water resources (Richardson *et al.* 1997, Van Wilgen *et al.* 1998). Holmes *et al.* (2000) have studied the recovery of South

African fynbos following alien woody plant clearing and fire. It is important that the indigenous vegetation recovers quickly. If not, the soils are susceptible to erosion and the further colonization by fynbos species is slow. An important strategy for restoring guild structure is to sow locally harvested indigenous seed in late summer or autumn, thereby augmenting the restoration of fynbos vegetation in restoration areas (Holmes and Richardson 1999). Although many of the sites are burned prior to restoration, it may be possible to use smoke technology to enhance the germination of many of the indigenous species. Another important consideration is that smoke technology can be used for habitat restoration in urban areas where fires are not desirable (Van Staden *et al.* 2000).

There is a great potential for the use of smoke in assisting the revegetation and restoration of mined areas. Roche *et al.* (1997b) used smoke techniques for the rehabilitation of bauxite mines in the jarrah forests in Western Australia. They found a 48-fold increase in total number of germinants and a 4-fold increase in species richness when smoke was applied to undisturbed jarrah forest. Although it is an important tool, the effectiveness of using smoke for revegetation will depend on the species composition of the topsoil seed bank (Read *et al.* 2000). Smoke treatments may be applied prior to sowing, or storage, as described earlier. A study by Enright *et al.* (1997) on *Eucalyptus* woodlands of Victoria has suggested that species which are not smoke-responsive are not adversely affected by smoke treatments. These findings support the use of smoke as a routine treatment for broadcast seed, a technique which is utilised by some Australian mining companies to improve the seedling recruitment and biodiversity within rehabilitated areas (Roche *et al.* 1997b, Lloyd *et al.* 2002).

A recent report by Rokich *et al.* (2002), following a study of woodland restoration in sand quarries in Western Australia, suggest that the application of smoke water sprayed over the soil surface is an effective means for broad-scale restoration. However, this method would require large quantities of smoke water and is not always very practical, although a preferable method to using aerosol smoke. Lloyd *et al.* (2000) have investigated the use of concentrated smoke products for the potential use of rehabilitating degraded landscapes. Results from the study suggest that concentrated smoke products could be economical and beneficial for broad-scale revegetation programmes.

Recent Research

As mentioned earlier, many of the more recent studies have investigated the size and spatial extent of the soil seed bank using smoke. By promoting seed germination with smoke (and heat), the assessment of soil seed bank samples is greatly enhanced, and species which require fire-related germination cues are less likely to be overlooked (Tang *et al.* 2003). Tang *et al*. (2003) used cold aerosol smoke and heat treatments on soil seed bank samples to determine plant distributions across the forest edges between subtropical rainforest and an adjacent eucalypt-dominated forest. Soil seed bank samples from a eucalypt forest, treated with cold aerosol smoke, showed a 4.3-fold increase in the level of germination within the first month (Read *et al.* 2000). The smoke treatment also significantly enhanced the rate of seedling emergence and increased the species richness. Results obtained from this study suggest that smoke and heat are important complementary factors in the promotion of germination by fire. A similar study by Enright and Kintrup (2001) showed that aqueous smoke was an effective treatment in enhancing the germination levels of soil samples from a heathy *Eucalyptus* woodland, although heat treatments also enhanced seedling emergence. A study on soil samples from a sand heathland (Wills and Read 2002) also demonstrated that heat, to a greater extent than smoke, was an important factor promoting seed germination, seedling density and species richness. These type of studies provide essential information for forest restoration, conservation, management and weed control, and illustrate the importance of investigating other fire-related cues along with smoke-stimulated germination.

The stimulatory effect of smoke may interact with heat and other fire-related cues. Many of the more recent studies, particularly by Australian researchers, have focussed on some of these interactive effects (Gilmour *et al.* 2000, Kenny 2000, Lloyd *et al.* 2000, Morris 2000, Morris *et al.* 2000, Tieu *et al.* 2001a). Gilmour *et al.* (2000) examined the effect of heat shock, smoke and darkness on the germination of the Tasmanian endemic *Epacris tasmanica*, and found that a combination treatment of these factors resulted in the highest levels of germination. A study on three *Grevillea* species found that both smoke and heat increased the germination, although the relationship between the two treatments varied with species (Kenny 2000). Similarly, Morris (2000) also found that smoke and heat treatments combined had an additive effect for four *Grevillea* species from east Australia. The investigation by Tieu *et al.* (2001a) on the interaction of heat and smoke on the germination of seven Australian species resulted in significant germination with a combined treatment for some species. Other recent studies on smoke-stimulated germination have included investigations on the grassy woodland and forest species in Australia (Clarke *et al.* 2000) and on the germination patterns and smoke responsiveness in artificially buried seeds of selected Australian native plants (Tieu *et al.* 2001b), the spatial and developmental variation in seed dormancy characteristics in the fire-responsive species *Anigozanthos manglesii* (Tieu *et al.* 2001c), and on factors affecting the germination of the Australian everlasting daisy *Shoenia filifolia* subsp. *subulifolia* (Plummer *et al.* 2001).

The recent research conducted by our group has focussed more on physiological aspects of smoke-stimulated germination than ecological aspects. Studies have included investigating the possible role of smoke in gibberellin metabolism (Gardner *et al.* 2001), the soluble sugars present during the germination of Grand Rapids lettuce seeds with different treatments (Jäger and Van Staden 2002), the dual nature of the regulation of Grand Rapids lettuce seed germination by smoke solutions (Light *et al.* 2002), and the possible role of nitric oxide in smoke-stimulated germination (Light and Van Staden 2003).

Conclusions

Through the research which we have conducted, over a number of years, we have attempted to isolate and identify the principal germination factor(s) in smoke (Van Staden *et al.* 1995a, 1995b). The water soluble chemical cues are highly active at very low concentrations — thus making the compound(s) extremely difficult to isolate and identify, and to date we have not been successful. We have also investigated various aspects of the physiology of smoke stimulated germination, in an attempt to gain a greater understanding of the various processes which may be involved (Drewes *et al.* 1995, Van Staden *et al.* 1995c, Jäger *et al.* 1996, Strydom *et al.* 1996).

Although smoke and aqueous smoke treatments are useful in a variety of applications, the elucidation of the compound(s) responsible for smoke-stimulated seed germination would be a major breakthrough. Furthermore, this would also aid in gaining a greater understanding of the physiological processes which are involved in smoke-stimulated seed germination. Continued research in this area is important to promote a further understanding of seed dormancy and seed germination — key research in terms of agricultural crop production and food security in South Africa.

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