The Role of Smoke in Dormancy Release for Horticultural Plants©

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Smoke plays a key role in the release of deep seed dormancy for a wide variety of plant species from a wide variety of ecological systems. Predominantly a feature of species from mediterranean-type vegetation in the mediterranean basin, chapparal from California, fynbos of South Africa, and the mediterranean and related vegetation types from Chile and Australia, smoke has proven to be critical for the germination of many deeply dormant species. Previous studies reported that heat and ash were thought to be the primary cues for release of dormancy and subsequent germination. However smoke, applied as an aerosol to unburnt bushland soil containing seeds of geosporous species or to seeds under nursery conditions can result in remarkable germination outcomes.

INTRODUCTION

In Australian native bushland habitats, application of smoke increased germination 42- to 48-fold greater than the control. The type of materials used to generate smoke, as long of plant origin and free from toxic or materials likely to be deleterious to germination (such as resinous or oily residues), can elicit a germination response. The action of smoke in releasing dormancy is unresolved for most species. In some cases smoke acts to increase the permeation of lipoidal deposits in the sub-testa whereas in other species, smoke has been found to denature inhibitor compounds in the seed endosperm and/or embryo.

Chemical(s) in smoke that elicit the germination response are highly water soluble, act at extremely low concentrations (nanogram levels), and are deposited on the soil surface following fire. The water soluble nature of the active principles in smoke means that for Australian bushland species for example, the first 25 to 50 mm of rainfall is sufficient to transmit the germination active principle to the level of the soil seed bank. Smoke can therefore be used to evaluate the in situ nature of the soil seed bank as well as act as a surrogate for ecological investigations of the dynamics of natural soil seed banks in fire-responsive plants.

For horticulture, smoke has been shown to act to stimulate the germination of a wide variety of plants from lettuce (where smoke replaces the red light requirement for germination) to some key Australian and South African plant groups. *Erica, Anigozanthos,* and restios are just some of the many species that possess smoke stimulated species. For any difficult-to-germinate species, smoke is a worthy candidate to test for dormancy breaking capacity even if fire is not part of the natural ecology of the plant.

PRODUCTS OF COMBUSTION AND THEIR ROLE IN PLANT GROWTH AND DEVELOPMENT

Fire in the wild is a key element in the restarting of ecosystems in many parts of the world. Deserts, heathlands, and woodlands from temperate to the arid zone often show remarkable adaptations to fire. Resprouting, flowering, germination, and enhanced growth represent some of the actions of fire in ecological processes. The Australian bush, African fynbos, and chapparal of California are often pictured with carpets of brilliant flowers and lush growth after fire leading to notions that the heat and ash from a fire have resulted in the germination response of many species. Smoke has now been found to be one of the more important elements enabling the release of seed dormancy in a wide range of pyric (fire-following) species.

The major products of fire that relate to ecological function include gaseous materials, nutrients (ash), heat, and smoke. Whereas research has focused on plant responses to nutrient and heat during and after a fire event, the other products of fire have until recently been mostly overlooked as having a key function in ecological processes. The remarkable fire-stimulated flowering in many mediterranean geophytes for example has been found for some species to be linked to the production of ethylene gas during the passage of a fire. Even the remarkable flowering in the Australian grass tree genus *Xanthorrhoea*, is linked to the production of ethylene gas resulting from a fire some 6 or more months earlier (Gill and Ingwersen, 1976).

NUTRIENT OUTPUTS FOLLOWING FIRE AS POTENTIAL GERMINATION CUES

Nutrients arising from the ash are commonly thought of as one of the most important components released after fire (Woods and Raison, 1982). Interestingly, ash has been implicated as a possible dormancy release cue for germination in some species. For example, nitrate washed out of the ash bed after fire has been demonstrated to most likely be related to nitrate activation of certain biochemical processes in the dormant seed (Baskin and Baskin, 1998). For Australian plants, records of nitrate-mediated dormancy release are rare (Bell. et. al., 1993; Bell, 1999; Lloyd et al., 2000; Lloyd, 2001) and it is likely that nutrient-linked dormancy release in seeds is not a frequent occurrence in nature.

SMOKE AS A CUE FOR GERMINATION

The role of smoke in germination is well established since the ground-breaking research by de Lange in his extensive investigation into the germination ecology of the rare South African species *Audouinia capitata*. For Australian plants, Dixon et al. (1995) resolved that smoke acted to promote germination for a broad range of native Western Australian species. Other studies (Roche et al., 1997a; Keith, 1997; Kenny, 2000; Morris, 2000) have shown that smoke acts across a broad range of Australian habitats, ecosystems, and phylogenetic groups with germination enhancements of between 42-fold (*Banksia* woodland, Rokich et al., 2002) and 48-fold (Roche et al., 1997b). Similar broad ecological linkages may occur in other countries where smoke-mediated germination events have been recorded.

The remarkable action of smoke in stimulating seed germination of dormant species is maximized for the native soil seed bank with the application of cooled, aerosol smoke for 60 min. When germination between smoke-treated and fired sites is compared, the same suite of geosporous species germinates however smoke elicits a higher number of germinants for each species — most likely due to the more effective deposition of smoke when artificially applied to soil compared to fire. When burnt sites are smoke-treated after passage of the fire, additional germinants are recovered equivalent to the maximum number achieved with the application of smoke alone indicating that patchy distribution of smoke following fire may result in only partial smoke deposition and elution to the soil seed bank.

Smoke can be applied in a number of forms and the general germination promotive effect of smoke points to this product of fire as being a key agent in the recruitment biology for many geosporous (soil seed bank) native species. The global array of taxa responding to smoke amounts to over 100 genera and 1000 species spanning many important horticultural families including Cyperaceae, Restionaceae, Dilleniaceae, Rutaceae, Myrtaceae, Proteaceae, Ericaceae, Haemodoraceae, and Poaceae.

The chemical species in smoke which stimulate germination of otherwise deeply dormant species are highly water soluble and are quickly eluted from the soil surface through to the soil seed bank. Such a rapid action requires that seed in the soil seed bank are in a state to be receptive to smoke uptake. In terms of the horticultural uses of smoke, seeds must be in a state to uptake smoke for promotion of germination. For some deeply dormant groups particularly in the Restionaceae (Australian groups and some South African species), Cyperaceae, Rutaceae, and woody fruited Ericaceae, smoke works more effectively when applied to the aged soil seed bank — either when seeds have been weathered in seed trays in the open for a year or directly to the natural seed bank. Research is underway to determine the role of aging in soil on the development of smoke receptivity in deeply dormant seeds.

Smoke has provided an important lesson in terms of the way seed biologists and ecologists can interpret the way fire operates in nature. However smoke provides benefits for species from environments not necessarily prone to fire with smoke responsive species recorded for Alpine Australian species, desert succulents such as mesembryanthemums, and some temperate rainforest species such as *Elaeocarpus* from south eastern Australia. A useful rule of thumb is if seed is intransigent to germination by other means then application of smoke may prove to be a beneficial line of research.

CONCLUSION

Smoke and the other features of fire such as heat, gaseous elements, and nutrients are features of fire that have been previously misinterpreted in fire ecology and fire management studies. The benefits of smoke for horticulture are considerable with commercial applications for a wide range of species already in use for which smoke has provided a remarkably high degree of germination performance. If you would like more information on the germination action of smoke contact the author. Trial packs of smoke water are also available for those wishing to undertake preliminary testing of smoke responsive.

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Plant Collection and Importation©

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Refugee French Huguenots started nurseries on Long Island fairly early in the colonial period, concentrating on tree fruits. John Bartram started the first North American botanical garden in pre-revolutionary times near Philadelphia. The international exchange of new plants for horticulture has classically been considered an unmitigated good. Many Old World crops, ornamentals, and weeds were brought to Arizona and the Southwest, first by the Spanish: e.g., olives, wheat, pomegranate, red brome grass, and later by the Anglo-Americans: e.g., eucalyptus, mulberry, citrus, cotton, and tamarisk. Arizona's nurseries, botanical gardens, and arboreta were instrumental in the introduction of non-native species into Arizona's ornamental horticulture: e.g., my institution, the Boyce Thompson Arboretum near Superior, was deeply involved in the introduction of species such as numerous *Eucalyptus* species, African sumac, various Australian *Acacia* species, *Aloe* species, etc.

Plant collection and importation in the past were quite informal. Permits were either not required or regulations were not enforced. One merely had to take seed out of a given country without declaring anything to the authorities. Similarly, seed and plants were often brought into the U.S. without any declaration at Customs. This situation began to change markedly about 25 years ago. At that time, international exchange of new plants for horticulture came to be considered as a qualified good thing.

The initial change came in relation to trade in endangered species, and was covered by CITES, the Convention on International Trade in Endangered Species, to which the U.S.A. is a signatory. This Convention covers both endangered plants and animals and is just now becoming deeply imbedded in the consciousness of Customs inspectors. Concern in this country about bio-safety issues has historically related to the introduction of noxious agricultural and horticultural weeds and diseases and has been regulated by the Animal and Plant Health Inspection Service - Plant Protection and Quarantine bureau (APHIS-PPQ) of the Agricultural Research Service (ARS). The Mission of APHIS-PPQ is to "safeguard agriculture and natural resources from the risks associated with the entry, establishment, or