proteinspotlight
> ONE MONTH, ONE PROTEIN <

Issue 216, July 2019
www.proteinspotlight.org

the scent of guile

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All kinds of strategies are used by living beings for their survival. Humans lay down traps to catch prey, chameleons melt into their environment to hide from predators and foxes cross water to bewilder those hunting them. Because of their inability to move, plants have devised the most elaborate ways of deceiving their environment in order to grow. They can exude scents or even produce fake fruit to attract pollinators for instance. They can also synthesize hosts of different molecules that, once released, fight off microbes. But there is yet another master plan used by many plant species as a means of defence. European maize, for example, is able to synthesize a molecule known as (E)-β-caryophyllene which is released by the plant's leaves and roots in the presence of larvae feeding on them. (E)-β-caryophyllene does not actually kill off the larvae but attracts yet other organisms that will feed on the herbivorous parasites, thus stalling harm that could be made to the plant. The enzyme at the heart of (E)-β-caryophyllene synthesis is a terpene synthase, known as TPS23.

Fig. 3.- Parte superior de una planta de teomaíz mostrando la colocación de las mazorcas cubiertas con sus hojas.

Indian botanist Pandurang Khankhoje

photo by Tina Modotti

The domestication of maize – from the Spanish *maíz* – began about 10 000 years ago in Mexico. It spread to the rest of South America in two major waves: the first across the Andes about 6000 years ago, and the second down into the lowlands about 4000 years later. Following the discovery of the South American continent by Christopher Columbus in 1492, Spanish settlers began to consume the indigenous maize and traders were fast to ship it back to Europe and introduce it to other countries. Thanks to its ability to adapt to very diverse climates, maize has been grown by farmers in almost every part of the world ever since and its by-products have become very popular. Corn is still part of a Mexican's staple diet, as it is now for populations in many parts of the world, namely Africa. The total global production of maize is actually bigger than that of wheat or rice. Besides being grown for animal fodder, corn flour and corn oil are consumed worldwide, and who hasn't had cornflakes for breakfast or popcorn with a drink. Or even tasted the odd glass of bourbon whiskey.

Growing maize on such a huge scale requires breeding skills, notably knowledge of how to ward off pathogens, insects and herbivores that can damage or even sometimes wipe away whole crops. Currently, hundreds of millions of metric tons of corn are produced worldwide every year – and as much as 30% of the world's maize crops are lost. In this respect, Mexican corn has a peculiar history of breeding. Pandurang Sadashiv Khankhoje (1884-1967) an Indian revolutionary and agricultural scientist almost accidentally landed in Mexico in the 1920s, where he discovered the need for Mexican corn farmers to learn how to improve the quality and yield of their crops. Initially appointed professor of Botany and Crop Breeding in the National School of Agriculture of Mexico, Khankhoje went on to lead the Mexican corn breeding programme before returning to his home country in 1955, several years after the declaration of Indian Independence. His work has been exquisitely recorded thanks to the Italian photographer and revolutionary political activist Tina Modotti (1896-1942) famous for her portraits of

Mexican labourers and peasants, and who Khankhoje met at the time. Modotti also took exceptional photographs for Khankhoje's monographs on maize and plant genetics.

Like all plants, maize has developed its own defence mechanisms: under threat, it is able to release cocktails of molecules such as benzoxazinoids, maysins and terpenoids. Terpenoids, for example, are found in resin and give off this particular bitter sweet fragrance we know. Such molecules protect the plants that produce them by being toxic or distasteful to herbivores, or may even attract another organism that will attack the herbivore itself. This is precisely one of the strategies used by European maize to kill off parasites: when larvae begin to feed on the corn's leaves or roots, they simultaneously set off the production and release of molecules able to attract above-ground level or below-ground level organisms, respectively, that feed off the larvae.

Terpenoids are modified terpenes – a large class of organic compounds produced both by plants and insects, which are important not only for defence mechanisms but also for cellular function and general development. By adding various chemical groups to terpenes, the resulting terpenoids have a structural and functional diversity that is multiplied by the thousands. The enzymes responsible for adding these functional groups to the terpene backbone are terpene synthases, or TPS, of which there are about 30 different kinds. In turn, each synthase is capable of synthesizing several types of terpenoid. (*E*)-β-caryophyllene is a terpenoid, and synthesized by European maize especially under attack by root parasites.

The enzyme responsible for the synthesis of (*E*)-β-caryophyllene has been coined Terpene Synthase 23, or TPS23. TPS23 catalyses the very last step in (*E*)-β-caryophyllene synthesis, i.e. the cyclization of farnesyl diphosphate. Surprisingly, (*E*)-β-caryophyllene is expressed differently in the corn's leaves or roots, which suggests that independent systems are used for the terpenoid's production above or below ground level, possibly via different regulatory promoters on the TPS23 gene sequence. (*E*)-β-caryophyllene, itself, also behaves differently depending on whether it is synthesized in response to parasites on the plant's leaves or roots. Leaf (*E*)-β-caryophyllene is volatile and acts with other compounds to attract parasitic wasps, for instance, which in turn oviposit on the larvae feeding on the corn. Below ground level, (*E*)-β-caryophyllene acts on its own to attract nematodes to parasites such as rootworm feeding on the corn's roots.

Talk about communication and strategy. Here are plants able to communicate with animals and make them wipe out a source of damage. Such strategies already present in Nature are inspiring for agricultural researchers, and provide alternative control options for smallholder farmers in countries like Africa and South America, for whom pesticides are too costly not to mention harmful. Transgenic methods are prohibited because of environmental issues but classical cross-breeding between maize species could do the trick and help farmers in North America, for instance, where maize seems to have lost the option of (*E*)-β-caryophyllene leaf and root defence. It is somehow always encouraging to realise that there is so much we can still learn from Nature – after all, she has been around far longer than we have.

Cross-references to UniProt

(E)-beta-caryophyllene synthase, *Zea mays* (Maize): B2C4D0

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Protein Spotlight (ISSN 1424-4721), http://www.proteinspotlight.org, is published by the Swiss-Prot group at the Swiss Institute of Bioinformatics (SIB).