A new theoretical approach to the selection of promising agents for biological weed control

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Abstract. A new theoretical approach to the selection of promising biological control agents that is based on the principles of an ‘evolutionary scenario’ is described using, as an example, the project on the biological control of tamarisk species (Tamarix spp.). The coevolution of host plants and phytophages is analyzed simultaneously for different groups (insects and mites) on the basis of a study of the history of the ecosystems, the genesis of the climate and palaeobotanical materials. Groups of genera that have evolved with one plant genus are distinguished. The phylogenetic levels of the taxa are studied in detail in connection with a possible transfer to new hosts as a result of the introduction of the agent into new regions. Transfer of phylogenetically-young species in the most advanced subgenera to phylogenetically unrelated groups of plants that have been connected historically with the evolution of dominants of ecosystems is shown for the first time. For instance, specialised genera of oligophages that have coevolved with the genus Tamarix include species that occur on Plumbaginaceae and Chenopodiaceae. The great majority of these oligophagous genera reveal no relationships with the closest family, Frankeniaceae. Each project includes information on the life history of each species, its noxiousness to the plant and its distribution, as well as available data on biotypes and host plants. A model of the ‘natural biological control’ in the palaeohistory of adventive weeds is proposed for the first time with reference to the migration of Asiatic, specialized oligophages of the genus Tamarix to the north and south of Africa by the end of the Neogene, as a result of the expansion of species of Tamarix caused by climatic changes.

Introduction

A new approach to the selection of potential agents for biological weed control has been developed that is based on the principles of an ‘evolutionary scenario’. During conventional host-specificity tests, potential agents are subjected to a wide range of test plants. Unfortunately, these tests cannot guarantee the safety of a particular agent for introduction. The ‘evolutionary scenario’ reduces the number of test plant species required for conventional specificity tests, and allows the inclusion of plant taxa that would not normally be used. The ‘evolutionary scenario’ incorporates a comprehensive investigation of ‘insect-plant relationship’ systems. New principles of ‘ecosystem evolution’, that are not typical of traditional Darwinism, permit an analysis of coevolutionary relationships between species of specialized phytophagous genera and phylogenetically unrelated plant taxa (Kovalev 1994, 1995a, b, c). The new approach is described, using as an example the project on the biological control of tamarisk species (Tamarix spp.) (Kovalev 1995a).

Methods

From the world literature, we analyzed all the oligophagous species that are found on members of the family Tamaricaceae. We excluded polyphagous species. Selected groups of phytophage genera then served as the main models for the study of coevolutionary pest-host processes. The model included several genera of insects and mites that are restricted to the genus Tamarix and whose evolution is presumed to have been governed by the evolution of the cenosis, or ecosystem, as a whole.

The elaboration of an ‘evolutionary scenario’ lead to more stringent conditions during the first stages of screening of potential biocontrol agents. This approach is less time-consuming and cheaper than conventional
procedures, in which promising agents are subjected to screening tests without a provisional analysis of insect-plant relationships and which results in a considerable increase in the number of test plants required during the final stages of the screening process.

We studied the palaeoclimatic history of the aridization of central Asia and Turan, daring and since the formation of the genus *Tamarix*. An ‘evolutionary scenario’ has been developed that can be used for the selection of potential agents from a complex of phytophages for introduction into North America and Australia for biological control of weedy saltcedars.

**Results**

Information on the distribution, life history, noxiousness of 325 species of insects and mites belonging to 88 genera, 33 families and 7 orders attacking tamarisks in the Old World is given, with reference to biological control of tamarisk:

(i) The global aridization in the Late Miocene (7.2 Ma) followed by and coupled with the Plio-Pleistocene cooling brought about the destruction of African tropical biota and the expansion of arid ecosystems, from deserts of central Asia (Northern Turan), along eastern Africa to South Africa (Kovalev 1995a). Botanists have traditionally regarded South Africa to be the home of the genus *Tamarix* (Baum 1966, 1978).

(ii) *Tamarix palaearctica* O. Kovalev was a particularly abundant species among fossil wood discovered in the Pliocene and Quaternary deposits of different regions of northern Africa. For several million years (5.5-2 Ma) fossil tamarisks blocked successions of local flora and formed stable associations, probably similar to recent associations of Asian salt cedars in North America.

(iii) Even in South Africa, recently-introduced tamarisks are exploited by species of tamarisk-restricted insect genera in the Cixiidae, Aphalarididae (Homoptera) and Apionidae (Coleoptera), which originated in central Asia. These insects migrated subsequent to the expansion of tamarisks and then contributed to the recent replacement of tamarisk forests by savannahs. Only a few, the most highly-specialized genera (*Colpocenia*, *Crassita* and *Corinaita*) reached South Africa. These genera are most promising for biocontrol and are recommended for introduction from central Asia. The absence of evolutionary radiation in these genera in South Africa over a long geological period is indicative of their stability and shows that they are safe for introductions elsewhere.

These insect genera have had an extremely important coenotic role because they have suppressed invasions of Asian tamarisks in Africa, which may be regarded as ‘natural biocontrol’. This biocontrol may be repeated by man using genera tested by nature.

In certain genera of insects that are restricted to tamarisks, some younger groups have been found in which phylogenetic relations with the host plants are of little importance. Surprisingly, these are insects from different families and orders (Cixiidae, Cicadellidae, Miridae, Chrysomelidae) attacking distantly-related plant families, (Tamaricaceae, Plumbaginaceae, Chenopodiaceae, and Fabaceae). The transition of the phytophages onto new host plants is attributable to the predominance of the plant taxa in the ecosystem and not to phylogenetic affinities of the plants. The great majority of these oligophagous genera reveal no relations with the closest family to the tamarisks, the Frankeniaceae.

Host-specificity in these phytophagous taxa is unstable and host-ranges may extend to many species in different genera. Also, these oligophages may belong to genera in which the majority of archean species were tamarisk-restricted and unable to exploit plants other than the Tamaricaceae. All this can occur within genera that embody species that are difficult to distinguish morphologically.

Different strategies are observed in endophagous groups that develop in galls or mines on a plant. Gall-makers and miners are indicators of the ecosystem-forming role of genera of predominant plants of the Cenophyte (Kovalev 1994). This is the highest level of phytophagous evolution. The ability to produce galls and mines is related to the rhythm of mobility of preimaginal stages of phytophagous insects. It has been erroneously thought that galls and mines have been permanent forms of plant injury for hundreds of millions of years beginning from the Carboniferous. However, we suggest that the first galls appeared about one hundred million years ago, i.e. in the early Upper Cretaceous, when they were represented by a wide diversity of forms.

Gall-makers are very important for biocontrol of weeds, not only as an indicator of the stability and specificity of a taxon, but for determining the primary range of a plant genus. A vivid example is the dandelion, *Taraxacum officinale* Wigg. Consensus exists among botanists as to the European origin of this
species with its primary distribution restricted to Scandinavia and central Europe. Botanists surmise that this species was introduced to America at the time of Columbus. We believe, however, that the genus *Taraxacum* originated in North America where it has coevolved with taxa of gall-forming insects that do not occur in the Old World. Presumably the genus *Taraxacum* penetrated the Old World from North America, possibly at the end of the Neogene, through Beringia, and gave rise to a large number of apomorphic forms. These forms have been described as valid species, with resultant taxonomic confusion. Gall-forming insects attacking tamarisks develop on a limited number of host-plant species and have been in existence without morphological change for millions of years.

All genera of tamarisk oligophages, except gall-makers, are currently restricted to the genus *Myricaria* as well. The absence of gall-makers on *Myricaria* spp. suggests that these species have been exploited by phytophages only relatively recently. For instance, the psyllid *Crassina tamaricina* is a gall-maker, whereas *C. myricariae* is not. Both feeding and development of some oligophagous species restricted to the genus *Myricaria* is possible on the genus *Tamarix* also.

**Discussion**

In practice, the criteria for selecting the best and safest natural enemies for *Tamarix* species would be as follows: (i) they do not attack *Tamarix aphylla*, a tree that is of value in the USA; (ii) they do not attack species of *Frankenia*, which is a native genus in the USA and Mexico; (iii) they cause considerable damage to the plant; and (iv) agents that attack different parts of the plant or that attack it in different ways should be selected.

The traditional methods for selection of the ‘best’ two or three candidate natural enemies require an extensive and expensive screening process to determine the specificity of the ‘candidate’, both in the field and, particularly, in the laboratory. Yet these experiments cannot always ensure that the agent will not switch from the target weed to other plant species.

The ‘evolutionary scenario’ model permits selection of a complex of more than 50 promising phytophages for use against *Tamarix* species with a certain guarantee of safety.

**References**


