FUNGAL BIOLOGY 120 (2016) 690–700

British Mycological Society promoting fungal science

journal homepage: www.elsevier.com/locate/funbio

The genetic landscape of *Ceratocystis albifundus* populations in South Africa reveals a recent fungal introduction event

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ARTICLE INFO

Article history:
Received 28 October 2015
Received in revised form
1 March 2016
Accepted 3 March 2016
Available online 11 March 2016
Corresponding Editor:
Joseph W. Spatafora

Keywords:
Canker
Emerging disease
Geographical range expansion
Host range expansion
Microascales
Microsatellite analysis

ABSTRACT

Geographical range expansion or host shifts is amongst the various evolutionary forces that underlie numerous emerging diseases caused by fungal pathogens. In this regard, *Ceratocystis albifundus*, the causal agent of a serious wilt disease of *Acacia mearnsii* trees in Africa, was recently identified killing cultivated *Protea cynaroides* in the Western Cape (WC) Province of South Africa. *Protea cynaroides* is an important native plant in the area and a key component of the Cape Floristic Region. The appearance of this new disease outbreak, together with isolates of *C. albifundus* from natural ecosystems as well as plantations of nonnative trees, provided an opportunity to consider questions relating to the possible origin and movement of the pathogen in South Africa. Ten microsatellite markers were used to determine the genetic diversity, population structure, and possible gene flow in a collection of 193 *C. albifundus* isolates. All populations, other than those from the WC, showed high levels of genetic diversity. An intermediate level of gene flow was found amongst populations of the pathogen. The results suggest that a limited number of individuals have recently been introduced into the WC, resulting in a novel disease problem in the area.

Introduction

Evolutionary mechanisms, such as host jumps or host range expansions, admixture effects, and fungal introductions have been shown to contribute to novel disease outbreaks by invasive alien pests including fungal pathogens (Anderson *et al.* 2004; Slippers *et al.* 2005; Desprez-Loustau *et al.* 2007; Stukenbrock & McDonald 2008; Giraud *et al.* 2010; Wingfield *et al.* 2015). In particular, expanded geographical ranges or fungal introductions into new habitats are two of the components driving the occurrence of novel diseases caused by either an adapted or selected fungal genotype with high levels of aggressiveness to new hosts (Desprez-Loustau *et al.* 2007; Pariaud *et al.* 2009).

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http://dx.doi.org/10.1016/j.funbio.2016.03.001
1878-6146/

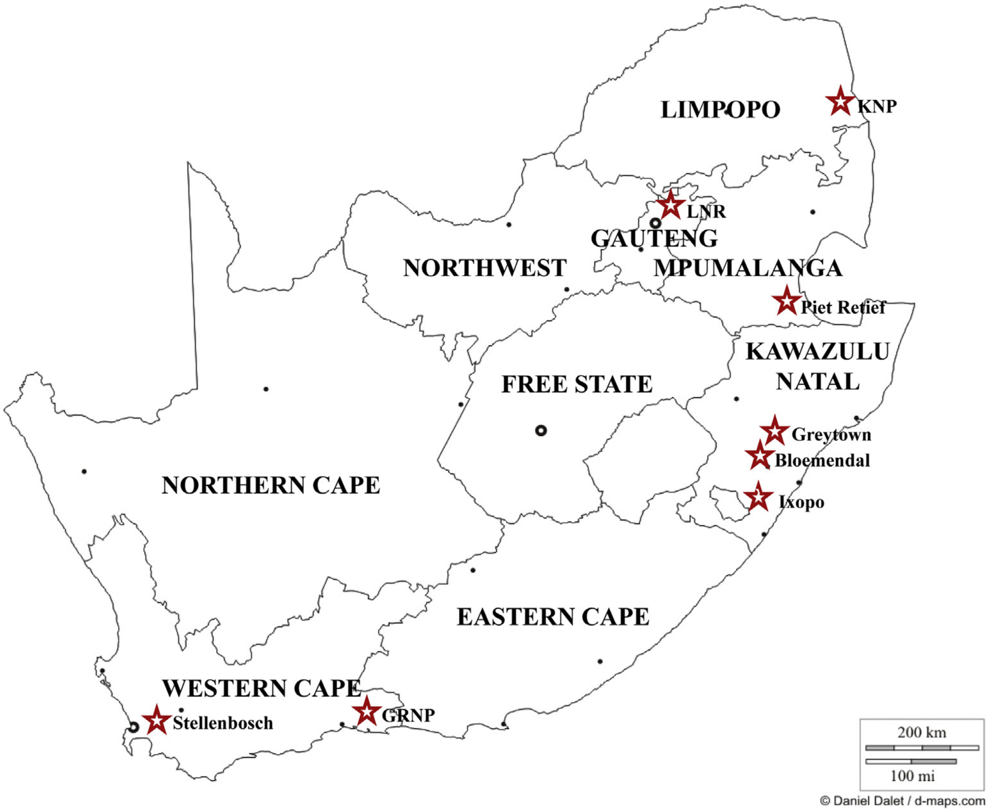

Fig 1 – Map of South Africa showing areas where *Ceratocystis albifundus* isolates were collected.

There are growing numbers of fungal or related pathogens that have been accidentally introduced into new forestry habitats, resulting in the emergence of novel fungal diseases. Some contemporary examples include laurel wilt disease caused by *Raffaelea lauricola* (Harrington *et al.* 2011), sudden oak death caused by *Phytophthora ramorum* (Grünwald *et al.* 2012), needle blight disease of pines caused by *Dothistroma septosporum* (Barnes *et al.* 2014), and wilt and die-back disease of *Acacia mangium* and serious mango decline on *Mangifera indica* caused by *Ceratocystis manginecans* (Tarigan *et al.* 2011; Al Adawi *et al.* 2014).

Species of *Ceratocystis*, as defined by de Beer *et al.* (2014), include many economically important fungal pathogens causing wilt and canker diseases on a wide variety of hosts, leading to substantial economic losses worldwide (Wingfield *et al.* 2013). One such species is *Ceratocystis albifundus* believed to be native to Africa (Roux *et al.* 2001, 2007; Barnes *et al.* 2005). This fungus was described as a novel species in the 1990's after it was identified causing a wilt and canker disease of non-native *Acacia mearnsii* trees and posing a significant threat to the sustainability of *Acacia* propagation in South Africa and neighbouring countries (Wingfield *et al.* 1996; Roux & Wingfield 2009).

Several lines of evidence exist to support the endemism of *C. albifundus* in southern Africa. It was initially isolated from a branch canker of native South African *Protea* spp. in Mpumalanga (Gorter 1977), and numerous other native South African tree genera including *Protea gaguedii* in the eastern part of the country (Roux *et al.* 2007). Generally, infections of these native hosts by *C. albifundus* are not characterized by disease (Roux *et al.* 2007), whereas it is highly virulent on nonnative *A. mearnsii* in plantations. Furthermore, population genetic studies showed a relatively high level of genetic diversity of *C. albifundus* populations in southern Africa, supporting the view that it is native to southern Africa (Roux *et al.* 2001; Barnes *et al.* 2005).

In 2008, *C. albifundus* was found for the first time on *Protea cynaroides*, native to southern Africa, and one of the commercially important shrubs cultivated for cut-flowers in the Stellenbosch area of South Africa (Bezuidenhout *et al.* 2011; Crous *et al.* 2013). Further sampling in 2013 revealed severely diseased *P. cynaroides* plants from the same production site on which the disease outbreak on *P. cynaroides* caused by *C. albifundus* had previously been reported. This raised several questions pertaining to the natural distribution of the pathogen in the country because *C. albifundus* had not previously been found in that part of South Africa. This suggested that the pathogen (i) could have been introduced into the Cape Floristic Region (CFR), (ii) has recently undergone a geographic range expansion or host range expansion to *P. cynaroides* in the CFR, or (iii) that selection for the cut-flower industry has resulted in a clone or small number of clones of *P. cynaroides*