1. INTRODUCTION

At up to 2000 Euros kg\(^{-1}\), fresh Périgord black truffles (the fruitbodies of *Tuber melanosporum*; hereafter truffle) are among the most expensive delicacies in the world (Martin et al. 2010). Moreover, their prices are expected to rise under projected climate change (Büntgen et al. 2012), because drought-induced reductions in Mediterranean harvests are contrasted by an ever-increasing global demand (Hall et al. 2003).

Truffles belong to a group of fungi that form a symbiotic association with the roots of a plant partner, known as ectomycorrhiza, wherein an extracellular sheath is formed through which nutrients and sugars are exchanged (Smith & Read 2008). In this mutualistic relationship, the truffle fungus is dependent on the plant partner for survival, reproducing sexually and in some cases taking over a decade to produce fruiting bodies (Thomas 2013). Importantly, the climatic conditions under which truffle mycorrhizae survive and grow differ from those that trigger their fruitbody production (Thomas 2014a). As such, the truffle fungi may exist in association with the plant-partners' roots but will not produce fruiting bodies unless local conditions allow.

Although much of the subterranean lifecycle and host interaction of this fungus is still unknown (Büntgen et al. 2015), its ecological range is assumed to be limited to calcareous habitats with a Mediterranean climate (Thomas 2014b). In Europe, natural and cultivated truffles are largely confined to a latitudinal range of roughly 40–48° N, with the most northerly report to date being near 48.7° N in Lorraine, France (Le Tacon 2017). It is argued that symbiotic host associations, amongst other biotic and abiotic parameters, restrict the geographical distribution and physiological plasticity of this ectomycorrhizal (and
gastronomic icon) species. At the same time, climate-induced range shifts along elevational and latitudinal gradients have been observed in a wide range of species from various taxa (Lenoir et al. 2008, Chen et al. 2011), including fungi (Kauserud et al. 2012, Boddy et al. 2014, Andrew et al. 2016).

2. FIND CHARACTERISTICS

Here we report on the first Périgord black truffle found in the UK. On 27 March 2017, a trained dog located a 16 g, ripe and pungent fruitbody of excellent quality (Fig. 1a,b). Microscopically (Fig. 1c) and genetically (PCR using the primers T.mel_for and T.mel_rev) confirmed (Bonito 2009), this unprecedented find describes the most northern and maritime Tuber melanosporum fruitbody ever cultivated. Inoculated and planted on former grassland in 2008, the host tree (Holm oak Quercus ilex) grows on previously acidic sandy-loam soil modified by agricultural liming to create a soil pH ~7.6. The site is located in south-east Wales (~52° N) at 96 m elevation with an approximate distance of 22 km from the sea. Established as a trial site to monitor the response of mycorrhizae to species-specific sub-optimal climatic conditions, the maritime climate is characterized by minimum, mean and maximum annual surface air temperatures of 5.7, 10.3 and 14.8°C, respectively. Cumulative annual sunshine and precipitation is 1427.9 h and 1076.9 mm, respectively (1981–2010 reference period).

Conditions for 2016, the year preceding our unexpected fruitbody discovery, were not exceptional (see https://www.metoffice.gov.uk/climate/uk/summaries/anomacts) and presented mean annual temperature, total annual rainfall and accumulated annual sunshine hours comparable to the 1981–2010 reference period.

3. IMPLICATIONS AND PROSPECTS

The successful truffle cultivation in south-east Wales not only challenges our understanding of the ecological requirements of hypogeal fruiting, but also implies the species’ ability to rapidly adapt to environmental changes and new habitats.

Temperature means and extremes, as well as sunshine hours and precipitation totals are all assumed to be important triggers for truffle production (Thomas 2014b). Mycorrhizae of Tuber melanosporum display some susceptibility to low winter temperatures but may still survive and grow in areas with a significantly different climate to the known truffle-producing range (Thomas 2014a). Truffle

Fig. 1. Study site and characteristics of the Tuber melanosporum fruitbody. (a) Plantation with the host tree (Holm oak Quercus ilex) at ~52° N (longitude withheld due to the sensitive nature of the site) and truffle dog. (b) Fruitbody showing dark blackish-brown asccarc with small pyramidal warts (upper right part) and a purple-black and marbled gleba (cross section) with thin while branching veins reddening upon exposure to air. (c) Ascus containing 1 to 5 opaque dark brown, ellipsoid ascospores ornamented with short pointed spines.
fruitbody production is less tolerant to variances in climatic and edaphic conditions (García-Montero et al. 2008) than truffle mycorrhizal survival, but here we show that fruitbody production can still occur over a much greater climatic range than previously assumed. Truffles are slow to develop, and for truffle fruitbody production in March, as presented here, the climatic conditions in the previous year are deemed to be important for the initiation, growth and maturation of fruitbodies. Throughout 2016, the regional climatic conditions of the study site were not exceptional when compared to the 30 yr reference period 1981−2010. Thus, our find most likely does not represent a direct response to inter-annual climate variation, but may instead be indicative of a longer-term, large-scale warming trend (Jenkins et al. 2008). In this regard, our find substantially challenges our understanding of the climatic tolerance of this economically important species.

Truffles are thought to have survived the last glaciation in a small number of refugia in continental Europe (Murat et al. 2004). Afterwards, the species colonized suitable areas of Europe, possibly by spore dispersal via mammalian vectors (Piattoni et al. 2012). However, colonization of the UK by species with such a spore dispersal mechanism would be dependent on land bridges, with the last land bridge connecting the UK and continental Europe having survived only until around 8200 yr BP (Weninger et al. 2008). It should also be noted that truffles are dependent on relatively mild winter temperatures, since their fruiting bodies mature during the coolest months and are quickly degraded by freezing conditions (Chevalier & Souzart 2012). Thus, even if truffles reached the UK during the last land bridge connection in the early Holocene, they would have had to endure long periods in which climatic conditions were probably not favourable for fruitbody initiation and maturation. Further, the truffle fungus is a slow-growing and uncompetitive species (Mamoun & Olivier 1993), and without sexual reproductive capability, it would have been disadvantaged in its ecological niche. Indeed, there is an absence of records of this species from the UK natural environment. However, recent and significant increasing seasonal temperatures have now created an environment in which truffle fungi may not just survive but also produce fruitbodies. Additionally, this species is dependent on terrestrial animals for spore dispersal (Piattoni et al. 2012), with no known records of avian interaction, and this combined with the island nature of the UK means that without human involvement, range expansion into this new and favourable climatic environment would have been challenging. *T. melanosporum* is now fruiting in the UK, thus local range expansion via animal vectors is possible; however, due to environmental specificity and competitive ability (Mamoun & Olivier 1993), this would likely be a very slow process that can be greatly enhanced by cultivation.

Much of England and Wales has a climate similar to our study site, so the prospects of truffle cultivation across large parts of the UK raise expectations to counteract some of the ongoing and predicted drought-induced southern European harvest failures (Büntgen et al. 2012). The potential impact of new cultivation attempts in the UK may be very significant, with a warmer climate having less influence in Atlantic regions where precipitation totals are expected to remain stable (EEA 2016). Moreover, the mild winter conditions of the British Isles imply a potential extension of the rather short Mediterranean truffle season by another 2 to 3 mo. Excluding climatic analysis, the global truffle industry has been forecast to reach sales of US$6 billion in the next 10 to 20 yr (Rupp 2016). As such, cultivation will have a clear and potentially sizeable economic benefit to the UK, whilst at the same time aiding the conservation of this icon species.

**LITERATURE CITED**


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