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RESEARCH ARTICLE

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Grass blindness

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Societal Impact Statement

Lolium temulentum (darnel) is an almost-forgotten species that combines the characteristics of a weed, a pasture grass, a cereal, a medicinal herb, a hallucinogen, a religious symbol, and a literary trope. The way in which darnel has disappeared from common experience and memory, particularly in the developed world, has lessons to teach about how passive and active influences can conspire to render people blind to the cultural significance of historically important plants.

Summary

Grasses, even those that feed the world, are easily overlooked. *Lolium temulentum* (darnel) is a grass species with a long history of human association; but, particularly in those countries with highly mechanised agriculture, it has physically and culturally faded from common experience. Archaeobotanical studies of Neolithic and early agricultural sites consistently find *L. temulentum* grains alongside remains of cereals. *L. temulentum* seeds are sources of potent psychotoxins, the products of endophytic fungi, and continued to enter the diet until modern farming methods and food hygiene regulations rendered the species effectively extinct in technologically advanced countries. *L. temulentum*, alone or in combination with other bioactive sources, was widely used in traditional medicines, often in ritualistic or religious contexts. Its status as a poisonous mimic weed of cereals made darnel a resonant literary trope for malignant subversion with which people would have been completely familiar in the pre-industrial era. The biblical parable about separating the wheat from the tares (tares was, possibly deliberately, an ambiguous alternative name for darnel) exerted profound religious and political force in the same period, and the Graeco-Roman belief that stress was able to transform wheat or barley into darnel persisted and justified some fundamental customs and laws of Judaeo-Christian culture. In the modern era, the not uncommon family or given name "Darnel," or some variant thereof, faintly reflects the rich history of *L. temulentum*; though it is likely that most possessors of such names will have long been rendered blind to the plant connection.

KEYWORDS

agriculture, cereal, darnel, evolution, *Lolium temulentum*, neolithic, poison, religion, weed

1 | INTRODUCTION

Some plants are born invisible, some achieve invisibility, and some have invisibility thrust upon them. Grasses are a case in point. They hide in plain sight. Grass is there in weed-rich turves (Figure 1), pristine sports surfaces, garden lawns, pastures, paddocks, rural landscapes, savannahs, prairies, steppes, but usually as a background for other more interesting objects, events and experiences. Grass species are

much of a muchness. Barriers to grass species interfertility can be flexible, if not downright porous, adding to identification difficulties. For example, hybridization between and within the genera *Festuca* and *Lolium* is rife, and in many cases recombination is promiscuous, with near homologous rates of pairing between homologous chromosomes (Grusz, Sigel, & Witherup, 2017; King et al., 2007).

Agricultural civilizations arose from the domestication of grasses that promised secure, storable sources of high-energy foodstuffs (Thomas, 2017). Evidence of the fundamental influence of grasses in human development can be seen in the very roots of language. The "grass-green-grow-graze" complex is a deeply embedded Proto-Indo-European reflex group derived from the ghrē-:ghrō-:ghrə- etymon (Pokorny, 1959). The ritual, symbolic status of domesticated grasses such as rice in Asia and maize in Central America is witness to the historically high degree of 'plant vision' in many societies.

Despite the fact that cereals continue to be dominant in the global diet (Kearney, 2010), the increasing distance of growing urbanized populations from the agricultural sources of their foods is having the effect of passively redacting plants from common experience. Furthermore, there are influences at work that combine actively to suppress awareness of particular plants within communities and societies. Here I discuss the history of a grass species that has had invisibility thrust upon it: *Lolium temulentum*.

2 | PHYLOGENY AND ARCHAEOBOTANY OF *LOLIUM TEMULENTUM*

The ryegrass genus *Lolium* comprises nine or ten species (the taxonomy is subject to periodic revision). All wild representatives are diploid, and most are allogamous (obligate outbreeders). *L. temulentum* (Figure 2) is one of a group of three weedy self-fertile (autogamous) species. The genus *Lolium* first diversified in the eastern Mediterranean region around 4.1 million years ago, splitting into an allogamous and an autogamous lineage, and the ancestors of present-day species had already begun to distribute along the Mediterranean Basin in pre-agricultural times (Inda, Sanmartín, Buerki, & Catalán, 2014). The most recent molecular phylogenies cluster the self-fertile *Lolium* species together (Cheng, Ma, Zhou, Humphreys, & Zhang, 2016; Guan et al., 2017; Inda et al., 2014; Figure 3). Autogamy is a loss-of-function trait. Introgression of autogamy from *L. temulentum* into the genetic backgrounds of allogamous *Lolium* and *Festuca* species has opened the way to mapping genetic loci that control self-incompatibility (Do Canto, Studer, & Lubberstedt, 2016; Thorogood & Hayward, 1992). In an important recent advance, the S-locus of obligately outbreeding *Lolium perenne* has been associated with a gene (functional identity not yet established) which, in self-compatible *L. temulentum*, has a frameshift mutation disrupting 24 amino acids at the C-terminus (Manzanares et al., 2016).

Estimates of the timeline of species divergence support a version of the origins of inbreeding *Lolium* weeds in which *L. persicum* invaded early cultivated fields and differentiated into *L. remotum* in flax and *L. temulentum* in cereals (Fuller & Stevens, 2017). As the result of co-selection for traits that constitute the cereal domestication syndrome, including self-fertility, *L. temulentum* became established as a potent mimic weed 'which was to haunt European farmers until the late Middle Ages' (Mabey, 2010)—an anthropophyte or what Fuller and Stevens (2017) call a "domesticoid." Archaeobotanical studies of Pre-Pottery Neolithic sites, principally in the Eastern Mediterranean region, have consistently found

FIGURE 1 *The Large Piece of Turf*, by Albrecht Dürer (1503). Mabey (2010) calls it 'painting's discovery of ecology'. From https://bit.ly/2B9QndV [accessed 14 August 2018], public domain via Wikimedia Commons

FIGURE 2 *Lolium temulentum*. Image by Franco Caldararo (http://tinyurl.com/pbgvdy5 [accessed 15 August 2018]), reproduced by kind permission of Professor Caldararo. The species includes both awned (as shown here) and awnless genotypes (Tominaga & Fujimoto, 2004)

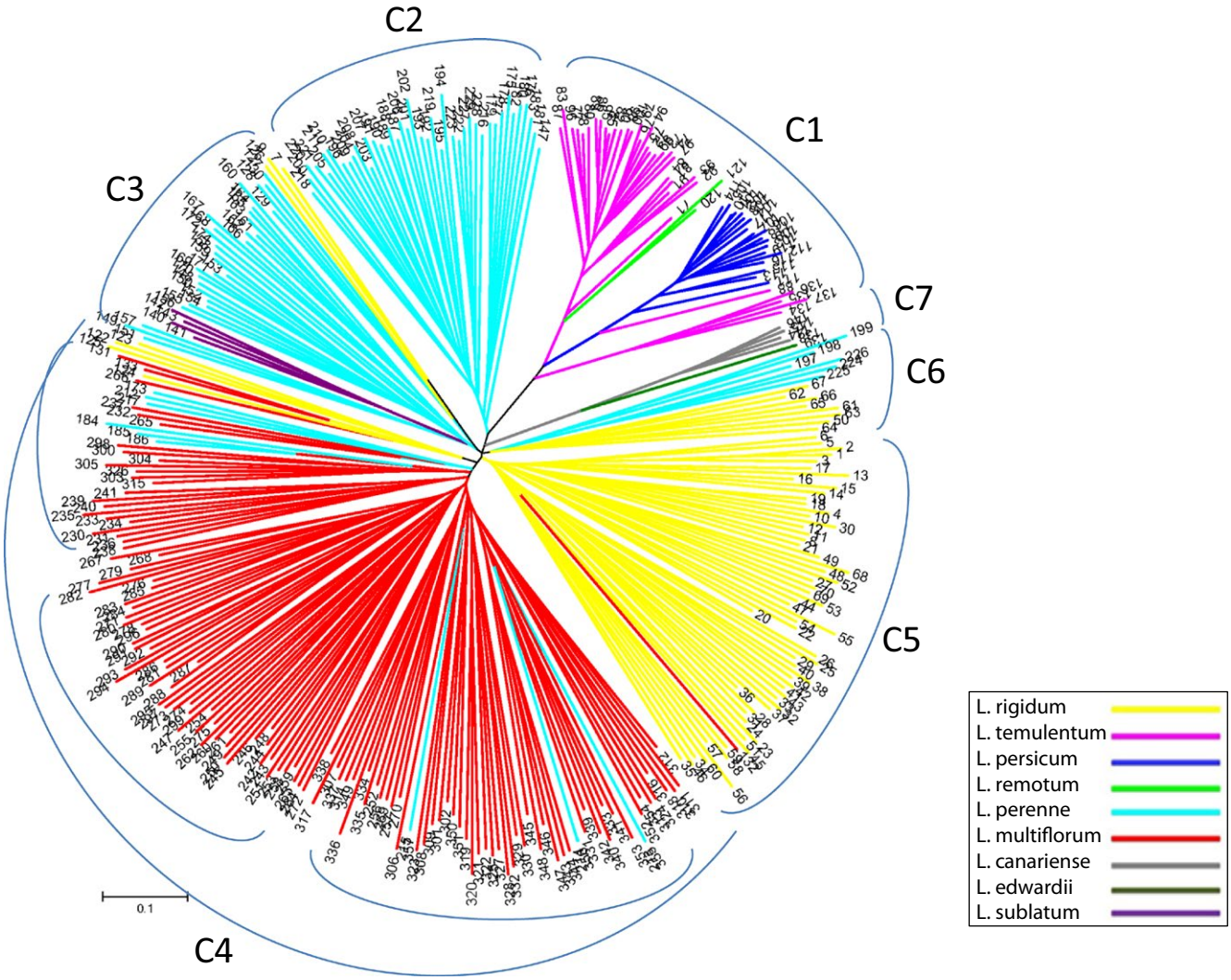

FIGURE 3 Unrooted neighbor-joining tree, comprising 357 individuals from 162 accessions of *Lolium*, according to 32 nuclear SSR markers, which groups the autogamous *Lolium* species (*L. temulentum*, *L. persicum* and *L. remotum*) in a distinct clade, C1. Reproduced from Guan et al. (2017) and published under a CC-BY license

remains of *L. temulentum* grains within cereal assemblages, and also in the preserved excreta of domesticated animals, dating as far back as 20,000 years BCE (Greenberg et al., 2017; Hartmann-Shenkman, Kislev, Galili, Melamed, & Weiss, 2015; Kislev, 2015; Koromila et al., 2018; Kotzamani & Livarda, 2018; Snir et al., 2015; Weide, Riehl, Zeidi, & Conard, 2018). The human-*L. temulentum* relationship is an ancient one, and *L. temulentum* was clearly entering the food chain in the earliest human settlements on a similar basis to other weeds like wild oat and rye (Fuller & Stevens, 2017; Harlan & de Wet, 1965; Ladzinsky, 1998); but unlike these species, it was never developed into a secondary crop species in its own right - possibly because of growing awareness of its toxic properties.

3 | BIOACTIVITY OF *L. TEMULENTUM*

L. temulentum is a rare example of a poisonous grass. There are accounts of its toxicity from the earliest periods of recorded human history (Thomas, Archer, & Marggraf, 2011, 2016). The grain often contains a melange of alkaloids and other secondary products with potent physiological and psychological effects. The source of these toxins is an endophyte (Kusari, Hertweck, & Spiteller, 2012; Schardl, Young, Faulkner, Florea, & Pan, 2012). Endophytic associations are now recognized as of widespread occurrence across grasses and other land plants. *L. temulentum* played a critical part in the history of this growing subject of research interest (Zheng et al., 2016): the first accounts of endophyte were observations on this species published at the turn of the last century (Guérin, 1898, Freeman, 1904; for further studies using current microscopy techniques, see Zhang et al., 2017). As well as providing phytochemical defences in return for nutrients, endophyte is now known directly to influence gene expression, development and stress responses in the host (Dupont et al., 2015), and evidence for horizontal gene transfer between endophyte and *Lolium* has recently been reported (Shinozuka et al., 2017).

Traditional medicine employs deliberate administration or consumption of herbal phytotoxins to invoke "eustress" according to the

principle of hormesis (Kaiser, 2003). *L. temulentum* has a long history of use as a hormetic treatment for a range of conditions (Teall, 2014; Thomas, Archer, & Marggraf, 2016): herbals dating back to the classical pre-Christian era tell us as much (for an entertaining survey of early herbals—including reference to *L. temulentum*—see Cooke-Trench, 1901). A particularly dramatic example of traditional medication containing *L. temulentum* is the preparation known as mithridate, a complex panacea credited with cure-all properties, especially canceling or expelling poison (Thomas et al., 2016). It was named after King Mithridates of Pontus, a first-century BCE ruler in the Black Sea region, who supposedly increased his immunity to poisoning by his enemies through self-administration of progressively stronger doses of toxins—a procedure called mithridatism. It was said that he became so tolerant that he was unable to commit suicide by poison and so his life was ended by the sword (Tsatsakis et al., 2018). Among the prominent historical figures to have been treated with mithridate was Federico da Montefeltro (1422–1482), a sufferer from severe attacks of gout (Fornaciari et al., 2018). Mithridate continued to be included in pharmacopoeias up to the nineteenth century.

Lewis-Williams and Pearce (2005) have argued that there is compelling archeological evidence for facilitated altered states of consciousness in the art and religion of Neolithic agricultural societies. As is generally true of narcotics from plant sources (Rätsch, 2005), there is a long tradition of deliberate, often self-administration of *L. temulentum* for the express purpose of achieving a state of intoxication. At the dawn of medicine, healing was the ritual responsibility of priests and shamanic practitioners, who would use bioactive herbs as entheogens. Records of *L. temulentum* used in this way as an opiate in Mesopotamia date from as early as 3,000 BCE (Teall, 2014); as an intoxicant in the pharaonic Egyptian feast dedicated to Hathor ("The Lady of Drunkenness"), commemorating the time when humanity was saved from destruction by beer (Goyon, 1992); and as a hallucinogen in the Eleusinian rituals of Classical Greece (Wasson, Ruck, & Hofmann, 1978). Accounts of the cultivation of *L. temulentum* expressly for boosting the inebriating qualities of beer, and for fraudulently adulterating bread, are recorded from ancient times to the brink of the era of industrialization (Thomas et al., 2016).

4 | THE VARIABLE NAMES OF *L. TEMULENTUM*

The number and diversity of common names for *L. temulentum* in many world languages are indicative of the everyday experience of people's encounters with the plant over the course of history. Names in English and Old English include Bearded darnel, Poison darnel, Annual darnel, Red darnel, Poison ryegrass, Darnel ryegrass, Ray-grass, Tares, Darnolde, Drake, Drawke, Drunk, Dragge, Sturdy ryle, Cheat, Wenwort, Chess, Virginian oat, Cokil, Cockle and Evir (Thomas, Archer, & Marggraf, 2011). Insofar as it is known at all today in the English-speaking world, *L. temulentum*'s informal name is darnel. The fluidity of plant vocabularies is a fact of historical life in botany, and it is frequently difficult to identify even approximately what species is being referred to in records pre-dating the Linnaean age. In the words of Dekker (2016), writing about weed evolution and ecology, 'A universal human trait includes behaviors to classify and organize the plants with which we observe, eat, utilize and interact. These traits arise from the way the human brain conceptualizes the world'. It follows that a proliferation of aliases is at best disorientating and at worst can be the stuff of fantasy.

The names of *L. temulentum* have been subject to such deformations from the earliest times. The principal classical sources on the subject of darnel are Pliny's *Natural History*, Dioscorides's *De Materia Medica*, and Theophrastus's *Enquiry into Plants*. A theme running through these works is a belief that one species can change into another, particularly when environmental stress compromises the harvest. Theophrastus states: "they say that wheat and barley change into darnel, and especially wheat; and that this occurs with heavy rains and especially in well-watered and rainy districts" (Theophrastus, 1916). This Graeco-Roman notion of species-to-species transformation became widely and persistently influential. For example, it informed Talmudic theory and, with reference to darnel (*zunin*) and wheat, appears explicitly in rabbinical literature. Shemesh (2017) quotes a Tannaitic debate about zunin in which it is asserted "They are a species of wheat, in which the fruit fornicate, as it is written: 'And the land shall not fornicate.' From here we know that the fruit fornicate." Such considerations underlie the Judaical laws of *kilayim* (prohibition of crossbreeding in animals, plants and humans).

In a world where transformation is unquestioned and forms a cornerstone of belief systems, little wonder that darnel became a symbol of mimicry, subversion and heresy (Thomas et al., 2016). Even *L. temulentum's* common name is mutable, casually appropriating that of quite different species. Shakespeare recognized the dramatic protean power of darnel (cockle) as a metaphor for betrayal and corruption (*King Lear*, *Henry VI Part 1*, *Coriolanus*; Archer, Thomas, & Marggraf, 2012). But perhaps the most momentous instance of fuzzy nomenclature in the relationship between *L. temulentum* and people concerns the religious and political upheavals of the 14th and 15th centuries, the consequences of which were still being felt centuries later. The focus was the Biblical 'sower parables' of wheat and tares (Matthew 13:24–30, 36–43; King James Version), where wheat represents the godly and faithful (those who read the Bible "correctly"), whereas tares stands for the heretic and schismatic (who read the Bible "incorrectly"). Tares in this context is a translation of ζιζάνια (*zizania*), the original Greek for darnel (Cousland, 2015); but tares has always been the name of a completely different species from *L. temulentum*, namely the legume vetch (*Vicia*). The sower parables were particularly identified with the English religious reformer John Wyclif, whose followers were called Lollards. The derivation of the latter name is not undisputed, but we (Thomas et al., 2016) have argued that there's a strong case to be made for its origin in *lolium*, the Latin for darnel. Confusing the issue by substituting "darnel" or "cokil" in the first

version of Wyclif's Bible (c. 1382) with 'tares' in the second (1394) was a measure to deal with dissent by disconnecting the Wyclif Bible from the Lollard heresy (Archer, Marggraf Turley, & Thomas, 2015). Darnel continued to be a prominent symbol of religious and political sedition for centuries to come. For example, the Gunpowder Plot of 1605, which sought to reinstate Roman Catholicism in the Protestant England of King James I, was vilified with the expression "Popish Darnell" (Gamage, 1613). In those days, everyone was acutely aware of what *L. temulentum* was and what it represented.

5 | *L. TEMULENTUM* IN THE MODERN ERA

The price, weight and quality of the bread and beer in England were legally regulated by the Assize of Bread and Ale from the 13th century until the law was repealed in 1863. From the late 19th century the food chain became increasingly subject to legislation (Wilson, 2008). Several circumstances contributed to this trend: growing awareness of the scale of adulteration, sharp practice and poor hygiene; improvements in chemical, biological and medical understanding of food and health; and the increasing expectations of the upwardly mobile post-Industrial Revolution classes (Collingham, 2017; Wilson, 2008). As this tide surged into the following centuries, it swept away people's experience and memories of darnel and the like. A certain Dr Eitner of Steinau gives an informative account of how it was in the mid-1800s. He was called to investigate illness in farm workers, who complained of burning in the mouth and throat and confusion in the head after eating food made from barley-meal. Eitner traced the problem to 'a large store of thrashed barley, so copiously mingled with darnel that at least every tenth grain was of this grass'. The report concludes 'it appeared probable that, in the above cases, serious results would have followed, but for the interference of sanitary police measures' (Periscope: Toxicology, 1850).

Where does *L. temulentum* stand today in relation to the general issue of plant blindness? In many countries it is a Red List species (for example Bleeker, Schmitz, & Ristow, 2007, Gauthier, Debussche, & Thompson, 2010). In others (for example, China; Huang, Wu, Bai, Zhou, & Wang, 2009) it is classified as a dangerous invasive. A survey of the status of this species in Slovakia is an instructive case-study (Eliáš, Hajnalová, & Eliášová, 2010). In their account of the history of *L. temulentum* in this region, the authors state that 'Slovenian ethnical groups living in western Hungary reportedly mixed the seeds of *L. temulentum* with those of barley to enhance the narcotic effects of beer'. By the millennium, as a consequence of enhanced seed cleaning techniques and herbicide application, *L. temulentum* had become a Red List species in Slovakia and northern Croatia (Turis et al., 2014), and was recorded as missing or extinct in Austria, the Czech Republic and Hungary. Having been driven from its traditional agricultural habitat, *L. temulentum* survives largely in scattered ruderal sites and remains critically endangered. Thus it is that the weight of history, myth, religion, societal change and technological advance have combined to thrust invisibility on *Lolium temulentum*. But there is a way in which it lives on, albeit covertly.

"Darnel(l)" is a common given or family name (see, for example, Smith & Conley, 1954) of English origin, as an online search for the unqualified term will testify. People surnamed Darnell account for about 36 per million of the current population of the UK, 66 per million in the USA and 12 per million in Australia. Genealogy sources agree that the name is directly derived from the plant and there is reason to trace some families to the Yorkshire village of Darnell, now Darnall, a suburb of Sheffield, where darnel was reputedly grown (Lower, 1860). According to the Internet Surname Database (www.surnamedb.com, accessed 19 August, 2018), the first recorded spelling of darnel as a family name in England is of one Godwine Dernel (1095, Abbey of Bury St Edmunds, Suffolk). Darnell as a given name is probably derived from the family name.

The surname 'Darnley' represents between 1 and 5 per million of the populations of the UK, USA and Australia. Of all the bearers of the name 'Darnley', one stands out as of particular significance in history and literature. The father of James I of England and VI of Scotland was Henry Stuart, Lord Darnley; the House of Stuart was, properly, the House of Darnley and Stuart. The "ley" element signifies "lea", hence a field (a "lea") of darnel: for example, in Stow (1580), the spelling of Henry Stuart's name is "Darnley" and "Darneley," and in the second volume of Holinshed (1587) it is "Darneleie." As ever, where there is darnel, there is treachery and toxicity (Thomas et al., 2016): Lord Darnley was murdered in 1567, an event of major political significance at the time and throughout the age of Shakespeare to the Stuart succession in 1603 and beyond. Hatfield (2004) has pointed out the parallels between the poisoning of Hamlet's father in Shakespeare's drama and the murder of Darnley. Furthermore, it is significant that one of Darnley's titles was Duke of Albany; in *King Lear*, Albany (an anachronistic character—the dukedom was first created in 1398, centuries later than the period of the play) is husband of Lear's daughter Goneril, and is cuckolded by Edmund. Archer, Marggraf Turley, and Thomas (2014) have discussed how, in *King Lear*, allusion to darnel, and the figure of Edmund—the "bastard," a contemporary term for a malignant weed—encode Shakespeare's interrogation of the Union of the Crowns.

Knowledge of *Lolium temulentum* is fading as intensive agriculture spreads and people, departing the land for the cities, become increasingly plant-blind. Its historical and religious significance may be subsiding into history, but darnel is preserved in the names of people, most of whom are unlikely to be aware of the richness of its meaning.

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