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The Australian truffle industry: History, challenges and opportunities

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ABSTRACT

Tuber melanosporum was first harvested in Australia in 1999, and exports began in 2007. Australia is now the world's fourth-largest truffle producer. The main challenges Australian producers face are climate change, obtaining well-mycorrhized seedlings with no contaminants, and preventing entry of the contaminant species *T. indicum* and *T. maculatum* to Australia and *T. brumale* from east to Western Australia. There is also increasing competition from other southern hemisphere countries. Almost all truffle orchards in Australia are in regions with 600–1500 mm annual rainfall and a mean daily mid-summer temperature below 25 °C. As soils in agricultural lands of Australia are frequently acidic, lime is applied to achieve the alkaline pH required by truffles. New truffle orchards should be planned bearing in mind future climatic predictions. The incorporation of more *T. borchii* and *T. aestivum* in truffieres, and the possible use of *T. magnatum* will spread the harvest period, and thus exports. Oaks and hazel are currently used as major hosts, and new host species are being investigated, including *Pinus*. The cost of establishing a truffiere in Australia is high. However, Australia lacks many pests, diseases, and social problems associated with the European industry, and together with being an environmentally friendly industry, these factors make truffle production an attractive agricultural investment in Australia which will aid regional economies.

1. Introduction

Truffles (*Tuber* spp.) are gourmet delicacies native to temperate northern hemisphere countries. As ectomycorrhizal fungi, they form symbiotic relationships with the fine roots of perennial host tree species such as *Quercus* spp. and *Pinus* spp., and produce hypogeous fruit bodies [1–3]. Bonito et al. [4] have estimated a minimum of 180 species. Ten species are commonly harvested for human consumption, the most valuable being *T. magnatum* Picco., *T. melanosporum* Vittad., and *T. aestivum* (Wulfen) Spreng. [5]. The unique and diverse aroma of truffles attributed to a complex mixture of volatile organic compounds (VOCs) is a key factor driving consumer fascination with this prized culinary ingredient. Truffles can exhibit a spectrum of aromas, ranging from earthy and garlicky to creamy, pungent, and even reminiscent of vanilla or cheese [6]. Europe has a long history of truffle cultivation, but the industry faces several problems constraining the expansion of production through the establishment of new trufferies and the continuation of harvesting from natural forests [7–10].

Australia was one of the first countries to establish truffieres outside the natural range of the *Tuber* species, with the initial production of *T. melanosporum* at the turn of the 21st century [11]. The Australian domestic market is still small, so growers export most of their crops. Data on total export production for all years is unavailable because truffle data was merged with data on other mushrooms for several years. However, Cullen [12] in 2021 reported, truffle exports were worth $30–40 million per year. Truffles from Western Australia (WA) account for 90 % of those exported [13], with 8.7 tonnes being exported in 2022, and exports are expected to increase to 20 tonnes by 2025 [14]. Australian truffles are exported to more than 60 countries in Europe, North America, and Asia [13–15]. Truffles are mainly exported fresh or chilled, but the local production of value-added products is increasing for export and domestic consumption.

This review covers the history of truffle production in Australia and the climatic and edaphic factors necessary for establishing this new industry. It examines past mistakes and how they can be avoided with the technology now available. It also details challenges to the industry,

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many of which are shared by other truffle-producing countries, and the opportunities to expand the industry in Australia.

2. Truffle production in europe and current problems

Truffles (*Tuber* species) have been harvested from native forests in Europe for centuries, but climate change, overharvesting, and poor forest management are resulting in a decline in yields from forests [7]. In the 1970s, efficient methods for producing mycorrhizal seedlings enabled the establishment of truffieres, principally in Mediterranean parts of southern Europe [16]. As many truffles from the forest and truffieres are traditionally sold in small quantities from numerous sellers at country markets, it is not easy to gauge the true total value of the European market. The global truffle market value in 2023 was estimated at USD 624.2 million [17]. In 2022, Spain produced 120 tonnes of black truffles, France 40 and Italy 30 tonnes [18]. As the main cultivated species will not thrive in areas with rising summer temperatures or extended dry periods, climate change is causing concern for European truffle growers [19–21]. In addition, there are problems of truffieres being invaded by native or introduced *Tuber* species of low or no value [22,23]. Thefts of truffles and truffle dogs, as well as deceptive dealers making fraudulent claims about the identity and origin of their products, have eroded farmers' confidence in the industry, and farmers are reluctant to establish new truffieres [8,9]. Moreover, in truffieres and native forests, host trees are being damaged by new or expanding pathogens such as *Phytophthora cinnamomi* Rands*, Armillaria mellea* (Vahl.) P. Kumm., *Rosellinia necatrix* Berl. ex Prill., and pests such as *Vesperus* spp., *Melolontha* spp., and *Anoxia* spp. [24,25]. The problems being experienced by the truffle industry in Europe open opportunities for truffle cultivation outside their natural range.

3. Truffle cultivation in Australia

3.1. History

In 1993, New Zealand was the first country in the southern hemisphere to succeed in the production of *T. melanosporum*. Australia quickly followed New Zealand, and the area of trufferies and truffle production in Australia now far exceeds that of New Zealand [26]. In Australia, in the early 1990's Dr Nicholas Malajczuk, a mycorrhizal expert working for the Commonwealth Scientific and Industrial Research Organisation (CSIRO) in Perth, WA, collaborated with truffle start-ups in Tasmania and produced *Corylus* spp. (hazel) and *Quercus* spp. (oak) with mycorrhizal roots after inoculating them with *T. melanosporum* [27]. Early producers in Tasmania included Duncan Garvey, Peter Cooper and Tim Terry, who made the first harvests of *T. melanosporum* in 1999 [11,28]. In 1997, Malajcuk, with a group of investors, established 13,000 inoculated hazel and oak trees in Manjimup, WA, on land with mainly loam soils. DNA analysis ensured the inoculum was *T. melanosporum*. Production of truffle fruiting bodies commenced five years later (N. Malajczuk, pers. comm.). The early development of the industry in Australia was heavily dependent on collaboration with truffle experts from Europe and America. These included Marcos Morcillo (Micrologia Forestal & Aplicada, Barcelona, Spain), Alessandra Zambonelli (University of Bologna, Italy), Christine Fischer (Forest Science Centre of Catalonia, Spain), Tom Michaels (Chucky, Tennessee, USA), James Trappe (Corvallis Oregon, USA) and the collaboration is continuing today. While international collaboration was welcomed, some growers undervalued the importance of sharing information within Australia to support the growth of the whole industry.

In Australia, cultivation has spread to New South Wales, Victoria, Australian Capital Territory, Queensland, and South Australia [11,29,30], and in total there are now more than 450 truffieres covering more than 696 ha. The exact areas and locations of all truffieres are not possible to document as many are small hobby operations, and data are only available for the 170 farmers that are members of the Australian Truffle Industry Association (ATIA) [31](K. Faull, President, ATIA, pers. comm.). The largest area of truffieres (>393ha) and the highest production is from Western Australia (WA). Exports began in 2007 and Australia is now the fourth largest producer in the world after Spain, France, and Italy [13,14,31–33] (A. Wilson, Great Southern Truffles, pers. comm.). Most truffieres in Australia are 1–5 ha, but the largest is 'Oak Valley Truffles' in Manjimup, WA, with about 38,000 trees across 75 ha [14](Fig. 1). In addition to *T. melanosporum, T. borchii* Vittad. is produced in Victoria and New South Wales, and *T. aestivum* in Tasmania and New South Wales (A. Wilson, Great Southern Truffles, pers. comm.; P. Stahle, former president, ATIA, pers. comm.).

3.2. Climatic parameters of truffle producing areas in Australia

In Europe, truffles are grown in southern regions with a mediterranean climate and calcareous soils [34]. Annual rainfall partly determines the regions where *Tuber* species may be cultivated (Table 1). However, for several reasons, the published annual rainfall data (Table 1) does not accurately delimit the areas suitable for each truffle species. Some truffieres may be irrigated in summer, and annual rainfall data do not indicate the spread of rain throughout the year. Records rarely come from a truffiere but from a weather station that may be many kilometres away. While there are data for many locations for *T. melanosporum,* fewer are available for the other species. *Tuber aestivum* and *T. borchii* are both known to be more drought-tolerant than *T. melanosporum* [35] (A. Zambonelli, pers. comm.). For all *Tuber* species, annual rainfall above 1500 mm may cause the rotting of truffles; however, *T. magnatum* requires the highest rainfall and has been recorded in areas with 2000 mm [11,36]. Recent studies have shown that summer dryness drastically reduces truffle production and the amount of *T. magnatum* and *T. melanosporum* mycelium in the soil [34,37]. In Australia, irrigation supplements natural rainfall in most truffieres and requires low salinity water and soil contouring that avoids waterlogging [38].

In Europe, the average temperature range for cultivating truffle species is -1.1 °C to 24.6 °C (Table 1). Considering the potential use of irrigation, temperature is more likely than rainfall to be the primary limiting climatic factor for truffle cultivation in Australia (Fig. 2). At present, almost all truffieres are in regions where the mean daily maximum temperature in mid-summer does not exceed 25 °C. Those in Western Australia above this isotherm have not yet been productive.

3.3. Edaphic requirements

The best truffle-producing areas have light, well-structured soil that remains stable when wet and is easy to dig by hand [43]. Within an area suitable for truffles, soil pH has the greatest impact on the natural distribution of truffle species [44]. Generally, truffles prefer an alkaline soil. In Europe, the soil pH for *T. melanosporum* ranges from 7.5 to 8.4 [3,45,46] 5.9–8.4 for *T. aestivum*, 6.4 to 8.7 for *T. magnatum* [3,5], and 6.5 to 7.8 for *T. borchii* [47].

Approximately half of Australia's 50 million hectares of agricultural land has surface soil pH values at or below 5.5. A significant portion (12–24 million hectares) falls in the extremely highly acidic category, with pH values at or below 4.8 [48]. Truffle farmers need to ameliorate soil acidity by adding large volumes of dolomite or lime to achieve an alkaline pH [11,49], but this is cost-effective for a high-value product such as truffles. Limed soil requires customised fertilisers to ensure adequate levels of iron, boron, copper, manganese and zinc for the host trees, and inorganic, organic and microbial fertilisers specifically for truffieres have been developed in Australia [49–51].

3.4. Host species

Hazelnuts (*Corylus avellana* L.) and oaks (*Quercus* spp.) are the major

Fig. 1. Oak Valley truffiere in Manjimup Western Australia (Photo credit – Adam Wilson).

Table 1
Climatic data for European locations where *T. melanosporum, T. magnatum, T. aestivum,* and *T. borchii* are produced. The highest mean daily maximum temperature for mid-summer (July) and the mean daily minimum temperature for mid-winter (January) are shown, together with the lowest and highest annual rainfall).

	T. melanosporum	*T. magnatum*	*T. aestivum*	*T. borchii*
Mean daily temperature maximum mid-summer July (°C)	23.2[a]	24.6[a]	24.6[a]	24.6[a]
Mean daily temperature minimum mid-winter January (°C)	1.6[a]	2.4[a]	−1.1[a]	0.1[a]
Minimum annual rainfall (mm)	400[b]	500[c]	514[a]	525[a]
Maximum annual rainfall (mm)	1500[d]	2000[c]	1500[d]	1500[d]

[a] [39], [b] [40], [c] [36], [d] [11].

hosts for truffles in Australia. Many farmers initially plant both hazelnuts and oaks, later removing the hazelnuts as the oaks mature [38]. Even though hazelnuts have the advantage of producing a second commercial product, some farmers avoid them due to their shorter lifespan compared to oaks, and challenges their root system pose in digging for ascocarps [52]. The main oak species utilised include English oak (*Quercus robur* L.) and French/Holm oak (*Q. ilex* L.) [38]. A wide range of oak species are utilised in America [53] and could be trialed in Australia. Host species being field tested with *T. magnatum* include oaks as well as poplars (*Populus*) and willows (*Salix*), which are used as hosts for *T. magnatum* in Europe [5,54].

4. Challenges for truffle production in Australia

4.1. Climate change

Projections from the CSIRO [55] for the future climate in southern agricultural regions of Australia include rising temperatures with a greater prevalence of extremely hot days and a decrease in extremely cool days. A decline in cool-season rainfall, leading to more frequent droughts, is also expected, while extreme rainfall events, high-intensity storms, and cyclones will increase. Fire danger will rise, with a greater number of high-risk fire days and a longer fire season. Significant year-to-year variations are also anticipated [55]. Many agricultural areas in southern Australia are already experiencing decreasing winter rainfall. For example, winter rain (May to October) in southwest Australia has declined by 20.5 % between 1960 and 2020 [56] and is expected to decrease by a further 6 % by 2030 and 12 % by 2090 [57]. Irrigation water for truffieres is mostly from farm dams, but during dry seasons, some farmers have faced shortages, leaving them unable to provide sufficient water for all their trees. An analysis of the effects of climate change on global truffle production predicted a 15 % decrease due to unfavourable climatic factors by the end of the 21st century [21]. The impact is expected to be felt more quickly in Europe than in Australia, which the analysis identified as one of the least affected areas for truffle production. In particular, truffle growing regions in eastern Australia are projected to see decreased rainfall in late autumn and early winter and increased summer rainfall. Coupled with less intensive temperature increases compared to Europe this may result in stable or even improved truffle yields [21]. Adapting to a drier climate will require changes in silvicultural techniques and the selection of host species and truffles provenances adapted to warmer, drier conditions. The heightened risk of wildfires necessitates careful planning of truffieres including the incorporation of appropriate fire breaks and strategically placed water points for fire suppression.

4.2. Production of inoculated seedlings and seedling evaluation

Producing high-quality inoculated seedlings is critical in truffle cultivation [10,58]. In 2012, Graham Duell, then president of the Australian Truffle Growers Association, reported only 10 % of the 150 truffle orchards established in Australia were producing commercial harvests, and more than 100 truffle orchards had yet to produce any truffles. It is thought this was due to poor inoculation of seedlings rather than orchard management, as 25.6 % of trees sampled in truffieres had no *T. melanosporum* mycorrhiza [59]. Contaminants, including *T. brumale* Vittad. have also contributed to low production from many truffieres in eastern Australia (P. Stahle, former president, ATIA, pers. comm.). In 2003, the Australian Consumer Protection Act was used to take a supplier of seedlings inoculated with the wrong mycorrhizal

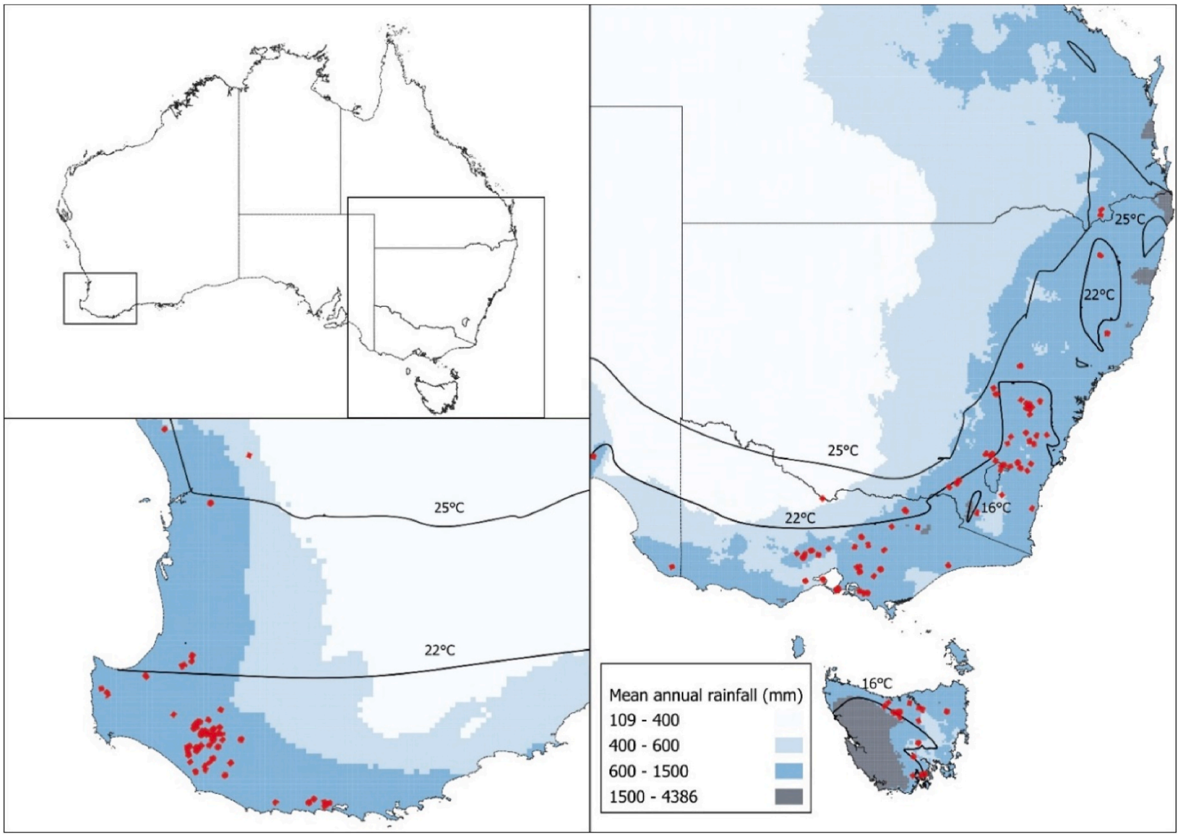

Fig. 2. Climatic parameters (30-year means, 1991–2020) of regions of Australia where T. *melanosporum* truffieres have been established. The 25 °C, 22 °C, and 16 °C isotherms indicate the highest mean daily temperature for mid-summer (January), and shades of blue indicate annual rainfall (mm). The climatic data are from the Australian Bureau of Meteorology [41,42]. Locations of truffieres are shown as red spots [31].

species to court, emphasising the necessity of having an agreed quality assurance system [11,60].

Previously, identifying mycorrhizal species on roots was challenging due to reliance on morphology. Now, DNA sequencing [61] allows for accurate identification of desired species, and metabarcoding can detect multiple fungal species in one sample. This technique can be used on spore slurries before inoculation and on mycorrhizal root samples from seedlings and established trees.

The Australian Truffle Industry Association established a seedling evaluation programme in 2013: the Australian Validated Seedling Tree Evaluation Program (AVSTEP) [62]. It is based on the Spanish program for *Q. ilex* seedlings inoculated with *T. melanosporum* and adapted for the host species used in Australia. Seedlings are assessed at around 18 months post-germination, and customers are provided information on their general health and the percentage of roots with *T. melanosporum* mycorrhiza. DNA analysis is used to detect the presence of contaminant *Tuber* species such as *T. indicum* Cooke & Massee*, T. brumale, T. maculatum* Vittad., *T. aestivum* and *T. borchii* and the presence, but not the identity of other ectomycorrhizal species [62–64]. However, there is scope for improving the speed, accuracy and cost-efficiency of seedling evaluation techniques, and new molecular tools applicable to the truffle industry are continually evolving [53]. In Australia, nurseries are still not required to assess their seedlings for acceptable levels of mycorrhization before sale, and until expert evaluation becomes compulsory, the industry will be constrained by ongoing problems associated with poor quality of planting stock, causing non-productive areas and the chance of introduction of undesirable species (P. Stahle, former president, ATIA, pers. comm.).

4.3. Novel aromas or flavours of the truffles

Geographic location, *Tuber* strain, and microorganisms associated with the truffle fruiting body influence the aroma profile [65]. This poses both a challenge and an opportunity for truffle producers in Australia. Imported *Tuber* ascocarps used for inoculations will carry some microbiota from their natural habitat, but Australia's unique soils introduce new microorganisms that may alter the truffles' flavor and aroma compared to European expectations [66]. Australian *T. melanosporum* truffles produce ~64 volatile organic compounds (VOCs), including 2,4-dithiapentane and dimethyl sulfoxide which have not been detected in *T. melanosporum* from Europe, and only previously been reported from European white truffles. The distinctive VOC compounds in Australian *T. melanosporum* truffles may be an advantage rather than a disadvantage as they add more desirable earthy, vegetal, herbal, and maillard aromas to the product. Overall, the knowledge of the VOCs produced by Australian *T. melanosporum* is poor. The survey by Choo et al. [66] was from only one farm in Manjimup, WA. Marco et al. [67] (2024) reported that there are more than 100 VOCs present in *T. melanosporum* worldwide. There appear to be no comparisons of VOCs of *T. borchii* and *T. aestivum* from Australia and Europe.

4.4. Prevention of invasion of truffieres by undesirable Tuber species

Certain inedible or low-value species of *Tuber* are 'pests' or 'contaminants' in truffieres [68]. For example, while *T. indicum* is valued in its native China, it is regarded as a contaminant in Italy and America, where it has been introduced. This is because it morphologically resembles the European cultivated species but is less desirable. There is concern that contaminated seedlings and global trade will allow it to spread further [69]. A 2012 survey of Australian truffieres did not detect

T. indicum [59]. It is essential to ensure that all imported truffles are accurately identified to prevent its accidental introduction. In British Columbia, three native *Tuber* species, *T. anniae* W. Colgan & Trappe, *T. beyerlei* Trappe et al. and *T. menseri* nom. prov. were detected in truffiers on hazelnut hosts [70]. Another contaminant species is *T. maculatum* in New Zealand, probably introduced to horticultural species before the advent of truffle farming. It has not yet been detected in Australia, but in New Zealand *T. maculatum* can outcompete the more valuable *T. melanosporum* [11], while in Italy, it can replace *T. borchii* [71], but coexists with *T. magnatum* [71]. *Tuber brumale,* which has a less desirable aroma, is a contaminant species in eastern Australia, particularly in Tasmania [23,38]. It is thought that *T. brumale* was introduced to the region through inoculum [23]. Its competitive ability varies under different environments. *Tuber brumale* may coexist or outcompete *T. melanosporum* and *T. aestivum* [23,72].

Contamination of undesirable *Tuber* species mainly occurs during the inoculation process. In the early days of the industry in Tasmania, dried spore powders were used as inoculum rather than fresh mixtures made from sporocarps. Unlike fresh truffle ascocarps, which can be evaluated before use, spore powders lack testing, increasing the likelihood of accidently introducing other *Tuber* species (P. Stahle, former president, ATIA, pers. comm.). Linde and Selmes [59] reported that in eastern Australian truffle nurseries, 8.2 % of seedlings were contaminated by *T. brumale*. It is difficult to eliminate once present and can only be controlled if detected early, and trees are pulled out and destroyed [69]. There are no reports of *T. brumale* in WA, and it should be theoretically possible to prevent its introduction as there are strict quarantine regulations concerning importing soil or plant material from overseas or eastern Australia to WA.

4.5. Threats from competitive native or introduced ectomycorrhizal fungi

Many trees and shrubs in Australia form ectomycorrhizal relationships, an adaptation to the low-nutrient soils, and most of the native ectomycorrhizal species form hypogeous fruiting bodies [73]. The abundance of ectomycorrhizal species in southwest Western Australia (SWWA) is particularly high: at least 2000 species have ectomycorrhizal roots or both ectomycorrhizae and arbuscular mycorrhizae [74]. It is estimated that over 70 % of the ectomycorrhizal species are endemic to SWWA [75]. Thus, depending on how long the area has been under cultivation and the distance from native forests, the soils of truffieres may have many native mycorrhizal species as well as introduced ones. Despite this the problem of competing native mycorrhizal species is not as great in Australia as in countries where oak and hazel are native. In Europe, 416, and America, 285 ectomycorrhizal species have been recorded in oak forests, and many will be in adjacent truffiers [76]. It is not known whether any endemic Australian mycorrhizal species are able to form mycorrhizas on the truffle hosts in the glasshouse or the field, but the introduced species *Hebeloma crustiliniforme* Bull. ex. St. Amans is known to compete with *Tuber* on hazelnut host trees in Tasmania [77]. *Hebeloma, Astraeus*, *Paxillus* and *Scleroderma* are common ectomycorrhizal species found in WA truffieres in Manjimup [78]. *Thelephora* was observed in potted oak seedlings in the glasshouse at Murdoch University [78], but the competitiveness of *Thelophora* in the field is still being evaluated. The application of lime can be an effective treatment to boost the competitive ability of *Tuber* species and reduce the abundance of acidophilic competitive ectomycorrhizal species such as *Amanita muscaria* (L.) Lam., *Boletus piperatus* Bull. (syn. *Chalciporus piperatus* (Bull.) Bataille), *Cenococcum geophilum* Fr., *Scleroderma mcalpinei* (Rodway) Castellano and *Scleroderma verrucosum* Vaill. ex Pers. [77,78]. However, healthy adult oak and hazel will host diverse ectomycorrhizal species. The optimal proportion of roots with ectomycorrhizas of *Tuber* and other species, as well as which combinations of species are beneficial and which are detrimental, is unknown.

4.6. Pests and pathogens of the host species and truffles

Slugs, slaters, beetles, and weevils are major pests that damage fruiting bodies at or near the soil surface and may also cause problems by blocking irrigation equipment [79]. The primary pathogens of host oak and hazel trees include the introduced root pathogen *P. cinnamomi* and the native fungal parasite *Armillaria luteobubalina* Watling & Kile. Both species are common in areas suitable for truffieres, and planting in infected areas should be avoided by analysing the soil microbiome before planting. *Euwallacea fornicatus* Eichoff (Polyphagus shot-hole borer) has been recently introduced to Western Australia [80], and is spreading despite the application of a quarantine zone around central Perth. Various *Quercus* species are hosts of this borer [81]. There is no effective chemical control and while pruning may help, often infected trees must be removed and destroyed. This pest poses a future threat to truffle cultivation. Some mammals, such as rabbits, pigs, and small marsupials, can damage tree hosts and both unripe and mature truffles. Endemic Australian truffles are an essential part of the diet of several marsupial species [38] and some native insect species [82]. Kangaroos are not known to consume truffles, but they can eat and kill newly planted host trees, while deer damage the bark of host trees. The control of mammalian pests is mainly done through fencing and baiting [38].

Australia is free of most bacterial and viral diseases of *Tuber,* which are present in Europe. However, the fungi *Ilyonectria macrodidyma* (Halleen, Schroers & Crous) P. Chaverri & Salgado and *Clonostachys rosea* (Link) Schroers, Samuels, Seifert & W. Gams are possible pathogens, and truffle rot (thought to be caused by *Trichothecium crotocinigenum* (Schol-Schwitz) Summerhill et al. [79,83,84] can be a problem in shallow truffles. Plant Health Australia has produced a biosecurity plan for the truffle industry. It focuses on identifying pests of truffles, risk assessment of these pathogens entering and establishing in Australia, and potential response and mitigation if they do enter Australia [85]. Western Australia has an advantage in that many of the pests and pathogens found in the eastern states have not yet been reported in the west [79,82].

4.7. Limited genetic diversity of hosts and truffles

Genetic diversity is crucial for a species' adaptation to environmental variables [86]. Growers need to plant inoculated trees that will persist for decades, so incorporating high genetic diversity in planting material is logical. The genetic diversity of *Tuber* in Australia was studied and although a bottleneck was expected, due to import of a limited number of sporpcarps for inoculation, the genetic diversity of *T. melanosporum* in Australia is similar to or higher than in its native habitats or Europe truffieres [59,87–89].

Genetic diversity in host tree species is also expected to be low as Australia has strict quarantine laws regarding importing plant material. Oaks in natural forests are largely outcrossing [90], but in Australia, oaks are frequently found as single specimen trees in amenity and domestic plantings and acorns are likely to result from selfing. Some inbreeding may occur as batches of seedlings often include many small and slow-growing individuals. On the other hand, hybrid oaks are possible when acorns are from an arboretum, and growers must be aware of this when assessing host seedlings. To better prepare for the impact of climate change (detailed above), focus should be on genetic material from the warmest productive areas in Europe when introducing either the hosts or the *Tuber* species.

4.8. Failure of trees to produce fruiting bodies

Although poor inoculation of seedlings appears to be the major contributing factor to low-yielding truffieres in Australia (see above), a shortage of male genotypes may also be important. The male gamete is thought to develop from spores, hermaphrodite mycelia, or short-lived saprophytic mycelium in the soil [91]. Unlike European soils, Australian soils lack a population of naturally occurring *Tuber* spores. Spores introduced during seedling inoculation are unlikely to remain viable in the soil during the non-productive years of the symbiosis, and it may be necessary to mechanically introduce spores (50 % of which should theoretically be genotypically male) into the soil under the canopy to achieve ascocarp formation [91,92]. The optimum timing, the best substrate, and the method of introduction require further research.

4.9. Costs of plantation establishment and lack of information about the longevity of production from truffieres

Establishing a truffiere in Australia requires high financial investment over many years before a return can be expected. Currently, establishment costs are estimated at AUD $30–60,000 per ha (without the cost of land purchase) depending on the density of host trees, how much liming is needed to ameliorate soil pH, and whether large dams are required for irrigation water. Annual maintenance is over AUD $2000 per hectare (M. McHenry, Silverplace Pty Ltd, pers. comm.). Oaks over 100 years old are known in horticultural settings in Australia, but the conditions required to maintain production levels of truffles from the host trees are unknown, as the oldest orchards are only ~35 years old.

4.10. Competition from other southern hemisphere producers and expansion of markets

The truffle industry in Australia has the disadvantage of long transport times to Europe and other overseas markets. Fresh truffles spoil rapidly, with changes in the composition of their aromatics giving them a shelf life of 7–10 days [93]. To maximise the use of their crops, as well as utilise imperfect truffle ascocarps, the truffle industry produces terrines, olives, honey, salsa, mustard, mayonnaise, nougat and pates [94]. Worldwide, value-added products are traded for more than twice the monetary value of fresh or chilled truffles, so this market is highly competitive [29].

Australian truffles are produced counter-season to Europe. *T. melanosporum* is harvested in Australia between late May and early August outside the European season of December to March [11], so there is no direct competition with Italy, France, Spain, or America [63]. However, producers in other Southern Hemisphere countries, such as Argentina, Chile, and South Africa, are strong competitors in Australia's market niche [63]. Private and government sectors in Chile have invested ~ US$800,000 and established more than 155,000 trees, mainly with *T. melanosporum,* on nearly 400 ha. These competitive southern hemisphere countries have an advantage over Australia in terms of lower costs for water, land and labour [63]. China will also be a major competitor in the markets for added-value products of *T. melanosporum*. The Hunan Academy of Agriculture produces 10,000 *T. melanosporum* mycorrhized trees annually, and truffles are produced in Guiyang, Sichuan, and Yunnan [95].

There is a need to increase Australian demand for truffles. Approximately 80 % of Australian-grown truffles are exported. There is no history of using truffles in Australian cuisine and extremely few shops will stock truffles during the season as local consumption is so low. Growers sell truffles directly to chefs in their local areas [63,96]. Truffle festivals such as the annual 'Truffle Kerfufle' in Manjimup, WA, and similar events in Canberra and Melbourne [93] are encouraging appreciation of their availability and desirability. Truffle hunting experiences are also a promotional tourist attraction.

5. Opportunities for truffle production in Australia

5.1. Diversification of Tuber species produced and use of additional host species

The expansion of the truffle industry in Australia may result from the greater use of *T. aestivum* and *T. borchii,* which have a wider natural geographic range and between them can tolerate higher temperatures and lower rainfall than *T. melanosporum* [35,44]. *Tuber borchii* and *T. aestivum* can also tolerate more acidic environments than *T. melanosporum* [3,45–47]. In addition, *T. aestivum* and *T. borchii* grow on a broader range of host species [53,97]. Currently, *T. aestivum* and *T. borchii* are produced in low volumes across Australia. Recent findings have shown that cultivating *T. magnatum* is possible in Europe [98], and this species is being tested in Australia, but as yet no truffle fruit body production has been reported [54]. Incorporation of these species into the industry will greatly expand the seasonality for exporting fresh truffles from Australia (Table 2).

In warmer areas, pecan (*Carya illinoinensis* (Wangenh.)K. Koch) may be a more heat-tolerant host for *T. aestivum* than oak [103,104]. Cultivation of *Tuber* species using the introduced *Pinus* species as a host is also an attractive possibility. Australia has large plantations of *Pinus radiata* D. Don and *P. pinaster* Loudon species owned by government agencies and farmers. Western Australia and Victoria have recently banned harvesting timber from native forests [105,106], so plantations of softwoods are now even more important. There is an opportunity to introduce *Tuber* species when establishing new pine plantations particularly on sandy soils, suitable for the growth of *T. borchii* and *T. aestivum.* In Italy, *T. borchii* is harvested from mixed forests of *Pinus pinea* L. *and P. pinaster* [97], and in Victoria (Australia), both *T. borchii* and *T. melanosporum* have been successfully produced under *P. pinea* (P. Stahle, former president, ATIA, pers. comm.). In North Carolina on *Pinus taeda* L., *T. borchii* produces fruiting bodies in a little over two years [107,108]. Research is needed regarding the survival and productivity of various *Tuber* spp. on *Pinus* species under Australian conditions, as well as how truffle and timber production can be co-managed on a commercial basis.

Introducing new *Tuber* species to Australia or expanding the areas under production with already established species raises the possibility of them spreading into established orchards of *T. melanosporum* or vice versa. More information is needed regarding the conditions under which one *Tuber* species might replace another and when more than one species can be cultivated in the same area. As additional species are added to truffieres, the possibility of accidental or deliberate sale of lower-value species morphologically similar to the more precious ones will

Table 2
Harvest seasons for truffle species in Europe and Australia.

	Month of harvest											
Truffle species(ref)	Jan	Feb	Mar	Apr	May	Jun	July	Aug	Sep	Oct	Nov	Dec
Tuber melanosporum[a,b]	+	+	+			×	×	×			+	+
Tuber borchii[a,c]	+	+	+	+	×	×	×	×	×			
Tuber aestivum[a,c]	×	×	×			+	+	+	(+)	(+)	(+)	(+)
Tuber magnatum[c]	+								+	+	+	+

×Harvest period in Australia (data for *T. magnatum* in Australia is not yet available), + Harvest period in Europe. Data for *Tuber aestivum* in Europe includes data for *Tuber uncinatum* (+) as molecular analysis has shown *T. aestivum* and *T. uncinatum* to be conspecific [99].
[a] [100], [b] [101], [c] [102].

occur if there is no screening for authenticity. Adding truffles to the Verified Provenance System [109–111] in Australia for high-value seafood and other products would be a preventive step. Significant investment in new testing technologies is needed to ensure traceability and inform consumers, preventing fraud from escalating as seen in Europe [9].

5.2. Methods of improving yields

One of the most successful traditional European methods to enhance truffle yields is the provision of 'Truffle traps', 'truffle wells' or 'Spanish wells'. These involve digging a pit under the canopy of a host tree and filling it with various substrates thought to attract mycelia, stimulate their growth, and enhance the chance of sexual reproduction. Spores are also usually added. They generally increase the truffle harvest and concentrate fruiting bodies in one area, simplifying the harvest [101, 112]. The effect of truffle wells is thought to be a combination of mechanical disturbance as well as the substrates used [101,112]. There are no scientific reports on the effect of mechanical disturbance or the use of truffle wells in Australia, but they offer an opportunity to increase production.

6. Conclusions

The truffle industry was initiated in Australia and New Zealand with collaboration from producers and scientists in Europe and America, and the foresight of Nicholas Malajczuk and Ian Hall, both of whom were scientists and developed inoculation methods while employed by government research agencies. The early years of Australian truffle cultivation experimentation depended on courageous, innovative farmers willing to collaborate with scientists. Initially, with some growers, there was a culture of commercial sensitivity, secrecy about techniques, and unwillingness to apply stringent quality assurance protocols to the production of inoculated seedlings. This constrained the broader industry from adopting the rapidly advancing research and knowledge available and contributed to the spread of contaminant species. An increasing proportion of growers now recognise the advantages of scientific research and collaboration to not only maximise opportunities, productivity, and quality but also to attract funding from government agencies to advance the industry. Currently, Australian government assistance is largely limited to a 150 % tax write-off. Better prices for the product might be achieved with a more organised cooperative export marketing system rather than growers acting independently as at present.

As with most agricultural activities, climate change is truffle growers' greatest challenge, particularly in Western Australia. Rain reduction can be tolerated if irrigation water is available, but rising summer temperatures pose the greatest threat. Problems in Australia with poorly inoculated seedlings will not be overcome until all producers agree to utilise the Australian Validated Seedling Tree Evaluation Program or a similar quality assessment standard. Pests and diseases are not major problems at present, but the contamination of orchards with undesirable *T. brumale* has occurred in the eastern states. Increased cultivation of *T. aestivum* and *T. borchii* will expand the harvest period for Australian truffles, and these species may be better able to produce under drier, warmer conditions.

Truffle farming is an environmentally friendly land use, with many biodiversity/carbon co-benefits and small requirements for agricultural inputs over time [113]. Australia has the advantage of being virtually a pristine environment for truffles, and with appropriate management and collaboration, the industry should be able to avoid many of the problems European producers face. Western Australia has the advantage of isolation from the eastern states and the possibility of excluding pests and contaminants that constrain production elsewhere. In common with truffle farmers worldwide, Australian truffle producers must attract greater investment to manage expansion within a changing environment and capture the many benefits that successful truffle cultivation can bring to regional economies.

CRediT authorship contribution statement

Mahesh C.A. Galappaththi: Writing – original draft, Investigation, Conceptualization. **Jen McComb:** Writing – review & editing, Supervision, Conceptualization. **Sarah J. Sapsford:** Writing – review & editing, Software. **Giles E. St J. Hardy:** Writing – review & editing, Supervision, Conceptualization. **Treena I. Burgess:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Consent to participate

Not applicable.

Consent to publish

All authors read and approved the publishing of this article.

Ethical approval

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Declaration of competing interest

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Data availability

Data will be made available on request.

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