

# Methane in Australian agriculture: current emissions, sources and sinks, and potential mitigation strategies

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**Abstract.** Methane is a potent greenhouse gas with a global warming potential ~28 times that of carbon dioxide. Consequently, sources and sinks that influence the concentration of methane in the atmosphere are of great interest. In Australia, agriculture is the primary source of anthropogenic methane emissions (60.4% of national emissions, or 3 260 kt<sup>-1</sup> methane year<sup>-1</sup>, between 1990 and 2011), and cropping and grazing soils represent Australia's largest potential terrestrial methane sink. As of 2011, the expansion of agricultural soils, which are ~70% less efficient at consuming methane than undisturbed soils, to 59% of Australia's land mass (456 Mha) and increasing livestock densities in northern Australia suggest negative implications for national methane flux. Plant biomass burning does not appear to have long-term negative effects on methane flux unless soils are converted for agricultural purposes. Rice cultivation contributes marginally to national methane emissions and this fluctuates depending on water availability. Significant available research into biological, geochemical and agronomic factors has been pertinent for developing effective methane mitigation strategies. We discuss methane-flux feedback mechanisms in relation to climate change drivers such as temperature, atmospheric carbon dioxide and methane concentrations, precipitation and extreme weather events. Future research should focus on quantifying the role of Australian cropping and grazing soils as methane sinks in the national methane budget, linking biodiversity and activity of methane-cycling microbes to environmental factors, and quantifying how a combination of climate change drivers will affect total methane flux in these systems.

**Additional keywords:** agronomy, methane, methanogenesis, methanotrophs, soil microbiology.

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## Introduction

Greenhouse gases (GHGs) absorb infrared radiation, thereby trapping thermal energy within the Earth's atmosphere. This has a direct effect on the global temperature. The global mean surface temperature has increased by  $0.6 \pm 0.2^\circ\text{C}$  over the 20th Century, primarily due to increasing concentrations of GHGs in the atmosphere (Forster *et al.* 2007). The Intergovernmental Panel on Climate Change (IPCC) estimates that mean surface temperatures will rise  $1.5^\circ\text{--}2^\circ\text{C}$  above the 1850–1900 temperatures by 2100 (Collins *et al.* 2013). Methane and carbon dioxide are GHGs. Methane has a global warming potential ~28 times that of carbon dioxide over a 100-year timespan and is estimated to contribute up to 20–30% of the global warming effect (Myhre *et al.* 2013). The concentration of global atmospheric methane has increased from  $715 \pm 4$  ppb in the 1750s, before the Industrial Era, to  $1\,799 \pm 2$  ppb in 2010 (Forster *et al.* 2007; Kirschke *et al.* 2013). This rate of increase

has differed over time, most noticeably with global atmospheric methane concentrations appearing to stabilise between 1999 and 2007; however, recently it has been noted that methane concentrations are rising again (Kirschke *et al.* 2013).

Global atmospheric methane concentrations are affected by a combination of natural and anthropogenic sources and sinks. Natural sources of atmospheric methane include anoxic soils, freshwater lakes, marine sediments, geothermal activity and enteric fermentation in the gastrointestinal tract (Crutzen *et al.* 1986; Hales *et al.* 1996; Luton *et al.* 2002; Webster *et al.* 2009). Several examples of anthropogenic activity involved in the release of methane to the atmosphere are the burning of fossil fuels, wastewater, biomass burning, landfill soils and agricultural sources such as rice paddy soils, livestock manure and enteric fermentation by domesticated ruminant livestock (Wise *et al.* 1999; Freibauer 2003; Shrestha *et al.* 2009). The increasing atmospheric concentration of methane is attributable

to increases in anthropogenic methane emissions (Denman *et al.* 2007a). In many countries, including Australia, agriculture represents the dominant source of anthropogenic methane emissions. The National Greenhouse Gas Inventory (NGGI) estimates that 60.4% of anthropogenic methane was produced from the agriculture sector between the years 1990 and 2011 (SEWPaC 2014). Over the same period, the other major sources were energy generation (26.1%), waste disposal and wastewater treatment (12.5%), land use, land use change and forestry (LULUCF) (1.9%), and industrial processes (0.1%) (SEWPaC 2014). Table 1 summarises Australian anthropogenic methane emissions in  $\text{kt year}^{-1}$ , also expressed as carbon dioxide equivalents ( $\text{CO}_2\text{-e}$ ) in  $\text{Mt year}^{-1}$  and as a percentage of total methane emissions. Agricultural methane emissions have been separated into the following fields as classified by the NGGI: prescribed burning of savannas, burning of agricultural residues, rice cultivation, enteric fermentation by ruminant livestock, and livestock manure management. The greatest contribution is from enteric fermentation (52.4% of total national anthropogenic methane), followed by the prescribed burning of savannas, typically for the conversion of land for agricultural purposes (5.9%).

Conversely, a combination of abiotic and biotic methane sinks exists, and these regulate the concentration of global atmospheric methane. It is estimated that up to 88% of global methane is photochemically oxidised with hydroxyl radicals in the troposphere (Cicerone and Oremland 1988). Approximately 3% of atmospheric methane diffuses into the stratosphere where it is also photochemically oxidised, 3% is oxidised by chlorine radicals from sea salt in the marine boundary layer, and 4% is aerobically oxidised by microorganisms in soils (Conrad 2009; Kirschke *et al.* 2013). It is estimated that soil microorganisms consume 30–60 Tg methane  $\text{year}^{-1}$  on a global scale (Dunfield 2007); however, the degree to which microorganisms facilitate methane oxidation in Australian soils, including semi-arid, arid and agricultural soils, is currently poorly understood (Dalal *et al.* 2008; Galbally *et al.* 2008). Indeed, under certain management regimes and environmental conditions, agricultural soils are less efficient sinks or may become net methane sources (Mosier *et al.* 1991; Mosier *et al.* 1998; Livesley *et al.* 2009; Livesley *et al.* 2013). Because microbial methane oxidation in soils can be negatively or positively affected by anthropogenic activities, careful consideration of the regulating factors of methane oxidation by these organisms is needed to contribute to maintaining a balance between global methane sources and sinks. The relatively large proportion of methane production from the agricultural sector makes this an important focus for understanding the mechanisms behind total methane flux and exploring potential mitigation strategies to both limit methane emissions and improve methane sinks. In this review, we briefly discuss the relevance of microbial functional groups involved in methane cycling, before focusing on several major contributors to Australian methane flux, including agricultural soils, biomass burning for agricultural purposes, rice cultivation, enteric fermentation and manure. Finally, we discuss the potential for total methane flux from agroecosystems to be affected by climate change factors.

**Table 1. Australian anthropogenic methane production between 1990 and 2011 (SEWPaC 2014)**  
Methane ( $\text{CH}_4$ ) units are  $\text{kt year}^{-1}$ ; carbon dioxide equivalents ( $\text{CO}_2\text{-e}$ ) units are  $\text{Mt year}^{-1}$  and converted assuming a methane global warming potential of 28; % is percentage of total annual methane emissions. National land use, land use change and forestry (LULUCF) values are not reported by National Greenhouse Gas Inventory between 1990 and 2008

Source	1990		1995		2000		2005		2011		Average	
	$\text{CH}_4$	$\text{CO}_2\text{-e}$ (%)	$\text{CH}_4$	$\text{CO}_2\text{-e}$ (%)	$\text{CH}_4$	$\text{CO}_2\text{-e}$ (%)	$\text{CH}_4$	$\text{CO}_2\text{-e}$ (%)	$\text{CH}_4$	$\text{CO}_2\text{-e}$ (%)	$\text{CH}_4$	$\text{CO}_2\text{-e}$ (%)
Total	5649	158.2	5297	148.3	5478	153.4	5307	148.6	5251	147.0	5396	151.1
Energy generation	1305	36.5	1304	36.5	1425	39.9	1449	40.6	1553	43.5	1407	39.4
Industrial processes	3	0.1	4	0.1	3	0.1	3	0.1	4	0.1	3	0.1
Waste	792	22.2	757	21.2	642	18.0	587	16.4	596	16.7	675	18.9
LULUCF	164	4.6	—	—	—	—	—	—	42	1.2	103	2.9
Agriculture total	3383	94.7	3231	90.5	3407	95.4	3198	89.5	3083	86.3	3260	91.3
–Prescribed savanna burning	234	6.6	283	7.9	387	10.8	315	8.8	362	10.1	316	8.9
–Burning agricultural residues	9	0.3	10	0.3	13	0.4	13	0.4	14	0.4	12	0.3
–Rice cultivation	24	0.7	31	0.9	35	1.0	10	0.3	15.7	0.4	23	0.6
–Enteric fermentation	3044	85.2	2823	79.0	2877	80.6	2794	78.2	2610	73.1	2830	79
–Manure	73	2.0	82	2.3	94	2.6	92	2.6	81	2.3	84	2.4

### Microbial functional groups involved in methane flux

Microbial metabolism is fundamental to the global methane cycle. Approximately 69% of atmospheric methane (345–414 Tg methane year<sup>-1</sup>) is a product of microbial methanogenesis, and it is important to note that atmospheric methane concentrations could be 60% greater than present concentrations if not for the consumption of methane by methanotrophic microorganisms in marine and terrestrial environments (Reeburgh 2007; Conrad 2009). Methanogens are members of complex microbial consortia involved in the anaerobic fermentation of biomass or geochemically produced substrates in environments such as wetlands, landfills, marine sediments, hydrothermal environments, wastewater treatment, permafrost, digestive tracts, and agricultural ecosystems such as rice paddies and cropping and pasture soils under anoxic conditions (Reeburgh 2007; Liu and Whitman 2008; Thauer *et al.* 2008; Conrad 2009; Drake *et al.* 2009). Methanogens are separated based on 16S rRNA gene phylogeny, morphology, carbon metabolism via methanogenesis, phospholipid fatty acid analysis, cell wall structure and growth conditions (Garcia *et al.* 2000). There are three documented pathways for methanogenesis. Hydrogenotrophic methanogens reduce compounds such as carbon dioxide and carbon monoxide (and formate in certain species) with hydrogen as an electron donor. Acetoclastic methanogens oxidise the carboxyl group of acetate to carbon dioxide and reduce the methyl group to methane through disproportionation. The final category, methylotrophic methanogens, utilise the methyl group of a wide variety of methylated C<sub>1</sub> compounds such as methanol, methylamines and methyl sulfides. The regulation, enzymes and thermodynamics of these pathways have been reviewed in detail elsewhere (Thauer *et al.* 1993; Deppenmeier *et al.* 1996; Liu and Whitman 2008; Lie *et al.* 2012). The orders Methanobacteriales, Methanosarcinales, Methanocellales (previously Rice Cluster I) and Thermoplasmatales are of particular interest to agroecosystems. Members of the Methanobacteriales and Methanocellales are typically hydrogenotrophic methanogens, whereas Thermoplasmatales are methylotrophic and the Methanosarcinales are metabolically diverse with identified species capable of acetoclastic, methylotrophic and/or hydrogenotrophic methanogenesis (Liu and Whitman 2008; Poulsen *et al.* 2013). Methanogens were once thought to be strict anaerobes (Hungate 1969); however, recent work has demonstrated that some species are aerotolerant (Erkel *et al.* 2006). Species belonging to the Methanosarcinales and Methanocellales are typically the most dominant methanogens in pasture and rice paddy soils under anoxic conditions (Angel *et al.* 2012; Scavino *et al.* 2013). Species belonging to the Methanobacteriales and Thermoplasmatales play an important role in the rumen of livestock (Wright *et al.* 2008; Kim *et al.* 2011; Poulsen *et al.* 2013).

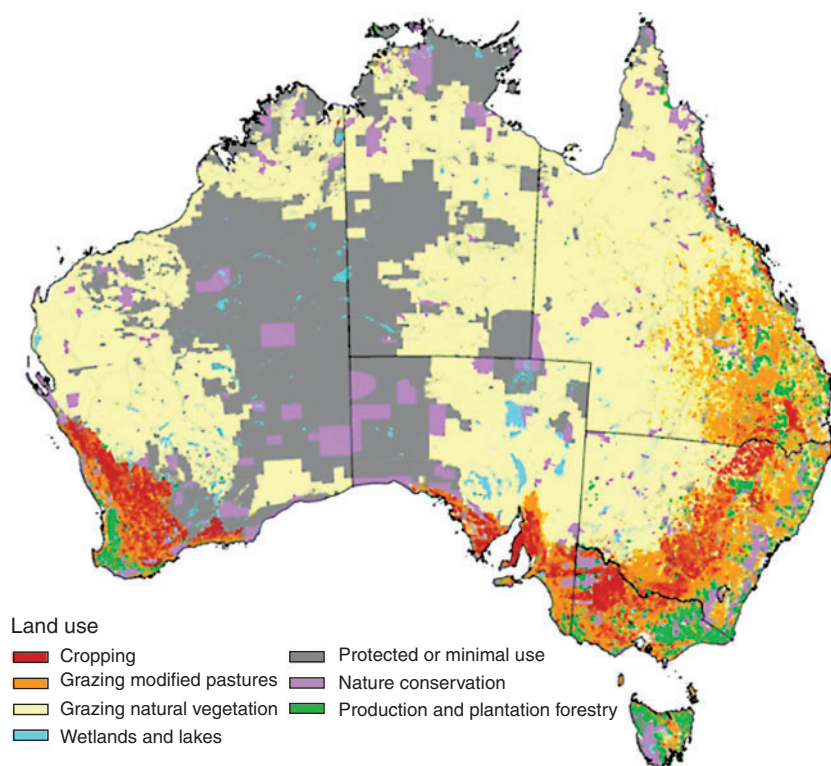
The other functional group involved in the methane cycle comprises organisms that oxidise methane and utilise it as a source of carbon (C) and energy, or methanotrophs (Hanson and Hanson 1996). This process can be performed anaerobically with sulfate or nitrate as electron acceptors by Archaea closely related to methanogenic Archaea in marine sediments, hydrothermal environments or wastewater (Hallam *et al.* 2003; Shima *et al.*

2012; Haroon *et al.* 2013), or with nitrite as an electron acceptor by ‘*Candidatus* Methyloirabilis oxyfera’ in freshwater sediments (Hu *et al.* 2009; Ettwig *et al.* 2010; Zhu *et al.* 2012). Alternatively, this process is carried out by aerobic methane-oxidising bacteria (MOB) with oxygen as the electron acceptor at the oxic–anoxic interface where diffusion of oxygen and methane meet (Trotsenko and Murrell 2008; Nazaries *et al.* 2013). MOB are the most pertinent bacteria involved in methane oxidation in agroecosystems, and this group shall therefore be the focus of this review. MOB are separated into several groups based on 16S rRNA gene phylogeny, phospholipid fatty acid analysis, morphological characteristics and C-assimilation pathways (McDonald *et al.* 2008; Semrau *et al.* 2010). The three dominant groups belong to the  $\gamma$ - and  $\alpha$ -Proteobacteria and the Verrucomicrobia.  $\gamma$ -Proteobacterial MOB of importance to agroecosystems include the *Methylocauldum*, *Methylococcus*, *Methylomicrobium*, *Methylobacter*, *Methylomonas* spp. and Upland Soil Cluster- $\gamma$  (USC- $\gamma$ ).  $\alpha$ -Proteobacterial MOB of importance to agroecosystems include the *Methylocystis*, *Methylosinus*, *Methylocapsa* spp. and Upland Soil Cluster- $\alpha$  (USC- $\alpha$ ). Currently, the only isolated Verrucomicrobial methanotrophs are extremophiles and shall not be focused upon in this review (Op den Camp *et al.* 2009). Two enzymes catalyse the first step in aerobic methane oxidation: a membrane-bound, copper-dependent, particulate methane monooxygenase (pMMO) (Lieberman and Rosenzweig 2004); and a cytoplasmic, copper-independent, soluble methane monooxygenase (sMMO) (Murrell *et al.* 2000). pMMO is ubiquitously expressed by MOB with the exception of the  $\alpha$ -Proteobacterial genera *Methylocella* and *Methyloferula* (Theisen *et al.* 2005; Vorobev *et al.* 2011). Unlike pMMO, the distribution of sMMO is sporadic, and it has been identified only from select isolates (McDonald *et al.* 2008). Both  $\gamma$ - and  $\alpha$ -Proteobacterial MOB can be classified as either low-affinity methane oxidisers (dependent upon methane concentrations >100 ppmv) or high-affinity methane oxidisers (1.7–30 ppmv) (Bender and Conrad 1993; Knief *et al.* 2006). It is suspected that low-affinity MOB mitigate the flux of methane entering the atmosphere from anoxic environments, whereas high-affinity MOB act as an active atmospheric methane sink (Shrestha *et al.* 2012).  $\gamma$ -Proteobacterial MOB appear to be the predominant group present in rice paddy soils (Bodelier *et al.* 2013). Agricultural or disturbed soils have a tendency to select for *Methylococcus*, *Methylocauldum* and *Methylocystis* spp. (Dorr *et al.* 2010; Nazaries *et al.* 2011; Ho *et al.* 2013). In undisturbed soils, such as forests, woodlands and grasslands, high-affinity methane-oxidising *Methylocapsa* sp., specific *Methylocystis* spp., USC- $\alpha$  and USC- $\gamma$  predominate, and it is these ecosystems that tend to be the most efficient methane sinks (Knief *et al.* 2003; Kolb 2009; Nazaries *et al.* 2011). Low-affinity methane-oxidising  $\gamma$ -Proteobacterial MOB are also present in these ecosystems and become active when methane is emitted from anoxic, methanogenic soil layers (Knief *et al.* 2006).

### Cropping and pasture soils

Much of Australia’s land is used for cropping and pasture–grazing (Fig. 1). As of 2005, in total, ~59% (456 Mha) of the

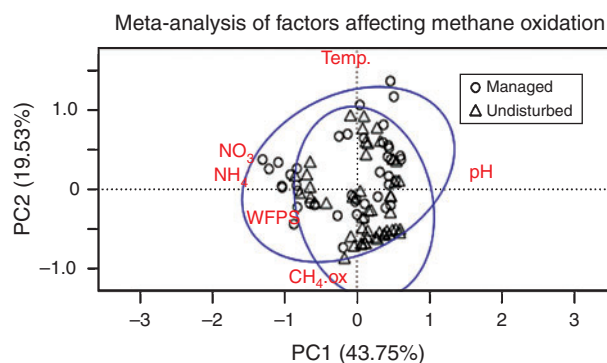




**Fig. 1.** Cropping and grazing land use in Australia. Image from the Australian Bureau of Agriculture and Resource Economics and Sciences (ABARES) (Sparkes *et al.* 2011).

continent is used for agricultural purposes, with 55.5% used for grazing, primarily on native vegetation in semi-arid and arid regions, and 3.5% used for cropping in south-western, south-eastern and eastern Mediterranean and temperate regions (Mewett *et al.* 2013). These soils important because they represent the largest potential terrestrial methane sink in Australia. Furthermore, as agricultural soils are less efficient methane sinks than undisturbed ecosystems, a thorough understanding of methane dynamics is required to develop appropriate mitigation strategies.

Several key factors regulate methane flux in soil: (i) soil moisture; (ii) temperature; (iii) ammonium and nitrate availability; and (iv) land-use change with regard to soil pH, substrate availability and electron acceptor availability. Figure 2 is a meta-analysis of 91 sites from 12 studies (Verchot *et al.* 2000; Merino *et al.* 2004; Suwanwaree and Robertson 2005; Jacinthe and Lal 2006; Fest *et al.* 2009; Singh *et al.* 2009; Galbally *et al.* 2010; Mapanda *et al.* 2010; Wu *et al.* 2010; Livesley *et al.* 2011; Zhang *et al.* 2012; Livesley *et al.* 2013) using principal components analysis (PCA). The interaction between soil moisture as water-filled pore space (WFPS, %), soil temperature ( $^{\circ}\text{C}$ ), ammonium ( $\text{NH}_4\text{-N}$ ,  $\text{mg kg}^{-1}$ ), nitrate ( $\text{NO}_3\text{-N}$ ,  $\text{mg kg}^{-1}$ ), soil pH and methane oxidation ( $\mu\text{g C m}^{-2} \text{h}^{-1}$ ) from these sites was compared with these factors as variables. Sites have been separated into two land-use types: managed sites (indicated by  $\circ$ ), which have been used for agricultural purposes or have been altered by human activity; and undisturbed sites (indicated by  $\Delta$ ), which have not been altered by human activity. The blue ellipses indicate



**Fig. 2.** Principal components analysis (PCA) of 91 sites from 12 studies comparing the interaction between water-filled pore space (WFPS, %), soil temperature ( $^{\circ}\text{C}$ ), ammonium ( $\text{NH}_4\text{-N}$ ,  $\text{mg kg}^{-1}$ ), nitrate ( $\text{NO}_3\text{-N}$ ,  $\text{mg kg}^{-1}$ ), soil pH and methane oxidation ( $\mu\text{g C m}^{-2} \text{h}^{-1}$ ) as variables. Sites are separated as managed sites ( $\circ$ ) and undisturbed sites ( $\Delta$ ). The blue ellipses indicate standard deviation (95% confidence) of the two groups. The plotted soil properties indicate the PCA loadings.

standard deviation (95% confidence) of the two groups. This meta-analysis was performed in this study, with statistical analysis performed in R version 3.0.2 with the package 'vegan' (Oksanen *et al.* 2013).

#### Soil moisture

Soil moisture regulates the diffusion (and therefore the availability) of methane and oxygen. Under conditions of high

soil moisture content, an increase in total methane flux is frequently observed (Bender and Conrad 1995; Dijkstra *et al.* 2011). This is due to a decrease in methane oxidation as oxygen diffusion decreases and MOB activity becomes limiting or to an increase in methane production as soil environments develop anoxic conditions and methanogens become active, or to both simultaneously. Conversely, low soil moisture content has adverse effects on atmospheric methane oxidation, possibly due to limited biological activity of MOB as a result of desiccation (Grosso *et al.* 2000). The question of what constitutes a 'high' or 'low' soil moisture content has no simple answer; it appears that microbial communities have adapted to local climatic conditions such that methane oxidation continues in desert soils of <10% soil moisture whereas methane oxidation is inhibited in meadow soils at 20% soil moisture (Strieg *et al.* 1992; Torn and Harte 1996). It should be noted that WFPS data were not available from these reports. Microcosm experiments have shown that oxygen penetration in moistened soil can be as little as 1.5–2.5 mm, at which point soils become oxygen-limiting and aerotolerant methanogens can be active (Angel *et al.* 2011). Because most Australian pasture soils are considered arid or semi-arid with an annual precipitation <400 mm (Morton *et al.* 2011; Haverd *et al.* 2013), the effects of soil moisture on arid and semi-arid ecosystems will be considered. Few examples of the effects of soil moisture on methane flux in these ecosystems exist. However, those that do suggest an optimum WFPS of 15–25% for semi-arid grasslands, where WFPS is a measurement of soil water content in relation to soil bulk and particle density (Mosier *et al.* 2008; Dijkstra *et al.* 2011). Interestingly, a study investigating the effects of WFPS on methane flux in Australian semi-arid eucalypt and wheat cropping soils suggested that watering or natural rainfall did not increase methane oxidation in soils with a WFPS <15%; indeed, precipitation actually increased total methane flux from the eucalypt soils (Galbally *et al.* 2010), possibly from anaerobic microenvironments within soil aggregates. Additional studies in Australian semi-arid and wheat cropping soils support the absence of a significant association between soil moisture and methane oxidation or MOB communities, although narrow ranges of soil moisture were noted (Bissett *et al.* 2012; Lam *et al.* 2013). In addition, no consistent correlations between WFPS and methane oxidation have been observed in Australian dry temperate woodland, tropical savannas or temperate pastures (Livesley *et al.* 2008, 2009, 2011). Those authors considered it likely that rapid water drainage in these soils reduced the impact of WFPS on methane oxidation, and studies of methane fluxes from sugarcane crops grown in floodplain soils with a WFPS consistently >60% may support this observation (Denmead *et al.* 2010). If the majority of the observed methane oxidation is due to atmospheric consumption by high-affinity MOB, then it is possible that WFPS may not significantly inhibit methane oxidation until soils become waterlogged and gas diffusion is restricted (60–100% WFPS). Figure 2 suggests a weak correlation between methane oxidation and WFPS, which may be due to the non-linear relationship between the two quantitative variables. Comprehensive analyses similar to studies by Dijkstra *et al.* (2011) and Mosier *et al.* (2008) of the effect of a wide range of WFPS on methane

oxidation in a variety of Australian dryland pasture and cropping soil types are required. Such studies should include pMMO transcription data to compare the activity of high- and low-affinity MOB under different WFPS and oxygen and methane concentrations.

### Temperature

Temperature has a profound effect on the thermodynamics and ecology of methanogens, respiration rates of organisms that produce substrates for methanogenesis, and methanotrophy (Conrad *et al.* 1987; Urmann *et al.* 2009). The change in free energy under standard conditions (25°C, pH 7.0, and gaseous hydrogen, carbon dioxide and methane at  $10^5$  Pa), or  $\Delta G^{\circ}$ , of hydrogenotrophic methanogenesis decreases with increasing temperatures above 25°C, which results in increased rates of methane production to generate the same amount of ATP mol<sup>-1</sup> methane (Conrad and Wetter 1990; Thauer *et al.* 2008). At low temperatures (4°C) and hydrogen partial pressures >10 Pa, acetoclastic methanogenesis predominates (Thauer *et al.* 2008). Similarly, the activity of mesophilic methanotrophs is dependent upon temperature, with a curvilinear response noted with increasing rates of methane oxidation between -5°C and 10°C, constant rates between 10°C and 20°C and decreasing rates >30°C (Dunfield *et al.* 1993; Castro *et al.* 1995; Borken *et al.* 2000). Because both temperature and oxygen availability are important for the regulation of methanogenesis and methanotrophy, temperature and WFPS are often shown to be the main variables explaining total methane flux (Wu *et al.* 2010). In semi-arid or arid soils, temperature influences the evapotranspiration of soil moisture (Borken and Brumme 2009). Examples of the effects of temperature in semi-arid soils suggest that temperature drives methane flux, particularly under conditions of low soil moisture (Wang *et al.* 2005; Galbally *et al.* 2010; Dijkstra *et al.* 2011). Figure 2 indicates a strong negative correlation between increasing temperature and methane oxidation.

### Ammonium and nitrate availability

The inhibitory effects of ammonium on methane oxidation are well documented, and appear to depend on nitrogen (N) source, soil inorganic N availability, methane:inorganic N ratio, application frequency and MOB community (Bodelier and Laanbroek 2004; Bodelier 2011). Inhibition at the enzyme level occurs in two ways, whereby ammonium can act as a competitive substrate for the active site of pMMO (Dalton 1977; Carlsen *et al.* 1991). Additionally, the oxidation of ammonium, ammonia and hydroxylamine by MOB produces nitrite, which may inhibit formate dehydrogenase, an essential enzyme for NADH production in the aerobic methane oxidation pathway (O'Neill and Wilkinson 1977; Jollie and Lipscomb 1991). These observations have been confirmed *in situ*, with significant inhibition of soil methane oxidation by the addition of 1–500  $\mu\text{M}$  ammonium g<sup>-1</sup> soil (Steudler *et al.* 1989; Adamsen and King 1993; Dunfield *et al.* 1995). The degree of inhibition is dependent upon ammonium and methane concentration, with the sensitivity of MOB to ammonium increasing in the presence of increasing methane between 1.7 and 100 ppmv (King and Schnell 1994a, 1994b). This may have

ramifications for terrestrial methane sinks as global atmospheric methane concentration increases. Strikingly, an application of  $45 \text{ g m}^{-2}$  of urea reduced methane oxidation rates by up to 41% over a 1-year period (Mosier *et al.* 1991), and other long-term studies suggest that ammonium inhibition persists for months to years (Willison *et al.* 1995; MacDonald *et al.* 1996). Similar to WFPS, methane oxidation rates can be improved by ammonium addition to N-limiting soils or inhibited when in N-rich soils (Steinkamp *et al.* 2001; Zhang *et al.* 2012). The composition of the MOB community is also important, because physiological variation between species exists for the oxidation of ammonium to nitrite, sensitivity to these respective compounds, and even growth stimulation in the presence of ammonium (Seghers *et al.* 2003; Mohanty *et al.* 2006; Nyerges and Stein 2009).

The mechanism behind nitrate inhibition is uncertain, and nitrate is in fact an important N source for MOB (Whittenbury *et al.* 1970). Like ammonium inhibition, nitrate interacts differently with specific species, with low-affinity MOB primarily inhibited with the application of  $1.7 \mu\text{mol g}^{-1}$  of nitrate fertiliser (Seghers *et al.* 2005). Denitrification of nitrate to nitrite by soil microbial communities may cause nitrite to accumulate in soils (Betlach and Tiedje 1981), especially at higher pH. Conflicting reports of nitrate inhibition exist, with some examples suggesting that nitrate has no effect on methane oxidation (Dunfield *et al.* 1995; Willison *et al.* 1995) and others suggesting highly sensitive responses to nitrate addition (Nesbit and Breitenbeck 1992; Bronson and Mosier 1994). If high-affinity MOB are insensitive to nitrate, and atmospheric methane oxidation is predominantly observed at certain sites, then nitrate addition is unlikely to affect total methane flux. Australian dryland ecosystems are typically characterised by low C and N availability (Bennett and Adams 1999; Cookson *et al.* 2006), and this applies to many pasture and cropping soils without fertiliser amendment (Weier 1999; Livesley *et al.* 2008; Galbally *et al.* 2010; Livesley *et al.* 2013). In cropping soils with  $90 \text{ kg urea ha}^{-1}$  or a combination of  $123 \text{ kg nitrate}$  and  $31 \text{ kg ammonium ha}^{-1}$ , total methane flux was close to 0 or became a net source of methane (Wang *et al.* 2011; Lam *et al.* 2013). There appears to be no direct correlation between methane oxidation and ammonium or nitrate concentration in soil (Fig. 2). This most likely reflects the complicated interaction between inhibitor concentrations, N source, application frequency, biophysical conditions regulating N transformation and the MOB species present in the soil community.

#### Land use

The conversion of land for the use of pasture or cropping is well known to reduce methane uptake rate. An analysis of northern European countries compared with international sites shows that methane flux of agricultural soils is consistently, on average, 71% lower than that of undisturbed sites (Smith *et al.* 2000). In addition to soil chemical properties, physical properties can also affect total methane flux. Soil compaction by livestock grazing or machinery increases the bulk density of soils and decreases soil macropore sites, consequently reducing gas diffusion (Sitaula *et al.* 2000; Jacinthe and Lal 2006; Liu *et al.* 2007). Compaction exacerbates the issue of soil anoxia after

precipitation events and drives methane flux towards becoming a net source of methane (Verchot *et al.* 2000; Merino *et al.* 2004; Teepe *et al.* 2004). Ploughing or conventional tillage of soils disrupts aggregates and disturbs soil microsites and the MOB community, and this may inhibit methane oxidation by up to 57% (Mosier *et al.* 1997; Hütsch 1998). The abundance and activity of MOB species is stratified *in situ* depending on the ratio of methane to oxygen (Reim *et al.* 2012), and so after disturbing this spatial distribution, it may take time for the MOB community to re-establish. In a typical Australian pasture system, it was hypothesised that the MOB community contributed to a decrease in methane oxidation efficiency compared with undisturbed sites (Livesley *et al.* 2009). Levine *et al.* (2011) have demonstrated that MOB diversity is linked to observed methane flux, and that agricultural conversion reduces both the diversity and activity of methane oxidation (Levine *et al.* 2011). Soils converted for agricultural purposes seem to select for low-affinity rather than high-affinity MOB (Chan and Parkin 2001; Kizilova *et al.* 2013), specifically for *Methylococcus* and *Methylocystis* spp. (Dorr *et al.* 2010; Nazaries *et al.* 2011). The mechanism behind the loss of atmospheric methane oxidisers in agricultural soils may be due to a combination of low C availability, increased fertilisation and soil disturbance reducing methane diffusion through compaction or tillage. Interestingly, an example exists of a semi-arid wheat field acting as a greater methane sink than an adjacent undisturbed eucalypt woodland (Galbally *et al.* 2010). Ammonium concentrations were similar between the wheat and woodland sites ( $1.62\text{--}5$  and  $2.2\text{--}4.5 \mu\text{g g}^{-1}$  soil, respectively), whereas nitrate concentrations were  $\sim 4$  times greater at the wheat site than woodland site ( $2.5\text{--}10$  and  $0.6\text{--}2.4 \mu\text{g g}^{-1}$  soil, respectively). Nitrate can be an important N source for MOB, and so it is tempting to speculate about whether N limitation in the woodland site resulted in lower methane oxidation rates. The authors noted that methane production by termites at the woodland site might have been responsible for the observed discrepancy in net methane oxidation between the sites (Galbally *et al.* 2010). This example is unusual and most evidence indicates that land conversion for agricultural purposes reduces methane uptake. In Fig. 2, the sites have been separated into managed (agricultural or otherwise disturbed) and undisturbed sites. A separation of the two categories based on the six variables examined is not apparent. Because methane oxidation in agricultural soils is, on average, two-thirds lower than undisturbed sites (Smith *et al.* 2000), it is possible that additional variables not included in this meta-analysis play a significant role in soil methane flux. These might include microbial and plant ecological factors. As more studies that compare biological and physicochemical factors emerge, statistical analyses including additional variables affecting methane oxidation will further contribute towards understanding the processes and mechanisms of methane fluxes and the practices that may enhance methane oxidation in different ecosystems.

#### Mitigation strategies

The most effective way to improve the methane oxidation potential of cropping and pasture soils is afforestation. This process appears to allow high-affinity MOB to re-establish



over time, primarily through improved gas diffusion–decreased compaction of soils, improved WFPS and the predominance of non-inhibitory concentrations of ammonium and nitrate (Hiltbrunner *et al.* 2012). After afforestation, it can take >100 years for methane oxidation rates to mirror that of undisturbed ecosystems, although as little as 31 years is sufficient under certain climatic conditions (Priemé *et al.* 1997; Smith *et al.* 2000; Allen *et al.* 2009; Nazaries *et al.* 2011). An analysis of methane oxidation rates between a native woodland, pasture and two plantation (18-year-old pine and 7-year-old eucalypt) systems demonstrated intermediate oxidation rates for the plantations between the woodland and pasture systems, with lower, but not significantly different, rates at the older pine plantation (Livesley *et al.* 2009). As of 2008, pine and eucalypt plantations in Australian temperate regions have been expanding at a rate of ~53 000 ha year<sup>-1</sup> and at that time were estimated to cover 1.82 Mha (MPIGF 2008). This is in stark contrast to national land use for cropping (27 Mha) and grazing, mostly extensive grazing (428 Mha) as of 2006 (Mewett *et al.* 2013), with conversion of woodland to agricultural or urban purposes at ~260 000 ha year<sup>-1</sup> (MPIGF 2008).

Although the most effective means to improve terrestrial methane sinks is through afforestation, there are soil management techniques to limit the inhibition of methane uptake in agricultural systems. The use of organic N sources (compost, manure) for fertiliser is preferable to inorganic N sources (ammonium, nitrate), because organic fertilisers do not appear to inhibit methane oxidation and may in fact stimulate it (Seghers *et al.* 2003; Skinner *et al.* 2014). Long-term application of ammonium to soils causes acidification and contributes to methane oxidation inhibition; therefore, liming to increase the soil pH can be an effective mitigation strategy (Hütsch 1998; Stiehl-Braun *et al.* 2011; Barton *et al.* 2013). Controlled-release fertilisers (CRFs), which utilise organic or inorganic N compounds with a low solubility, or fertilisers coated in hydrophobic polymers may be a viable alternative; however, to the authors' knowledge the long-term impact of CRFs on methane oxidation has not been evaluated (Chen *et al.* 2008). Crop rotation with N<sub>2</sub>-fixing legume species can improve N uptake by crops and methane uptake rates (Barton *et al.* 2013). Improving soil N retention through the use of the urease inhibitor N(n-butyl)thiophosphoric triamide (25 µg g<sup>-1</sup> soil) strongly inhibits methane oxidation (Bronson and Mosier 1994). However, conflicting reports exist concerning the impact of nitrification inhibitors such as 2-chloro-6-trichloromethyl pyridine and 3,4-dimethylpyrazole phosphate on methane oxidation rates (Bronson and Mosier 1994; Weiske *et al.* 2001).

No-till management practices are being adopted across Australia to reduce fuel and labour costs, improve soil moisture retention and sequester C in or reduce C loss from the topsoil (Maraseni and Cockfield 2011; Page *et al.* 2013). As no-till systems reduce the amount of soil disturbance, this practice has been shown to significantly enhance methane uptake in <5 years (Hütsch 1998; Six *et al.* 2004). Contradictory reports of other methods of soil C sequestration exist, such as with the application of biochar, with examples showing both negligible and significant decreases in methane

oxidation (Spokas *et al.* 2009; Scheer *et al.* 2011). Where methane oxidation was reduced, as little as 2% (w/w) biochar applied to soil incubations, which equated to field applications of 24 t ha<sup>-1</sup>, was enough to inhibit the activity of MOB (Spokas *et al.* 2009).

Unfortunately, it is difficult to make generalised, quantifiable recommendations on how potential methane uptake can be improved, because of the complexity of MOB activity *in situ* and a limited dataset. In order to evaluate properly the effectiveness of Australian cropping and pasture soils as a methane sink, additional measurements considering the discussed environmental factors in relation to long-term mitigation and farm management practices must be made.

### Biomass burning

The burning of plant biomass results in the thermogenic production of carbon dioxide and hydrocarbons, including methane (Wang *et al.* 2013). This is a non-microbial, abiotic process. Carbon dioxide, rather than methane, is the primary product of biomass burning in the field (McCarty 2011). The amount of direct emissions from biomass burning is a function of the fuel load (dry weight in Mg ha<sup>-1</sup>), the area burnt (ha) and the efficiency of the burning (Henry *et al.* 2005). Biomass burning for agricultural purposes is separated into two categories: the prescribed burning of savannas, and the burning of agricultural residues.

#### *Prescribed savanna burning*

The primary purpose of the prescribed burning of savannas is the conversion of grasslands and woodlands to pasture. Converted pastures are of a higher nutrient quality than degraded pastures and are therefore more suitable for livestock (Kaur *et al.* 2006; Radford *et al.* 2007). Approximately 50% of Australia's forest biomass occurs in commercial rangelands reserved for grazing and pasture (Dean *et al.* 2012). It has been suggested that since European settlement, 11% (21.9 Mha) of forest biomass has been cleared, through burning or other means, for agricultural purposes (DEWR 2007). Biomass burning leads to direct emissions of methane dependent on the factors outlined above, and smouldering residues continue to release large quantities of methane (up to 130 µg C m<sup>-2</sup> h<sup>-1</sup>) over a subsequent 24-h period (Livesley *et al.* 2011). Although burning results in direct emissions of methane, once the system returns to a pre-burnt steady-state, methane oxidation by the MOB community is not necessarily affected (Castaldi *et al.* 2006). Indeed, active methane oxidation can recommence as little as 2 days after burning (Poth *et al.* 1995). Reports on the post-burning effect of fire on soil methane flux in savannas and seasonally dry ecosystems are contradictory, with significant increases, decreases and no impact on methane oxidation observed from various studies (Poth *et al.* 1995; Priemé *et al.* 1997; Castaldi *et al.* 2006; Livesley *et al.* 2011; Inclán *et al.* 2012). Total methane flux remains more dependent upon temperature and WFPS, with burnt soils displaying a general trend of transiently increased temperature and decreased WFPS; therefore, climatic conditions, soil properties and plant–microbe associations on a local scale determine MOB activity after burning (Inclán *et al.* 2012). Interestingly,

in savannas where termite activity is a source of methane emissions, frequent burning may contribute to decreased termite methane emissions and significantly increased total methane uptake (Poth *et al.* 1995; Castaldi *et al.* 2006). A better understanding of how Australian MOB communities respond to fire, increased temperature and decreased WFPS, particularly in dryland ecosystems, is required to evaluate properly how fires affect total methane flux.

The prescribed burning of savannas may not affect soil methane flux post-burning; however, as stated earlier (see *Land use*), land converted for agricultural practices is roughly one-third as effective at oxidising methane as undisturbed sites (Smith *et al.* 2000). As such, prescribed burning and naturally occurring fires lead to short-term, direct emissions of methane, but total long-term methane flux likely remains undisturbed unless post-burnt savannas are converted to cleared grazing pasture. Unfortunately, the improved nutrient capacity of pasture soils in post-burnt fields becomes negligible within several decades (Dean *et al.* 2012), and as described previously (see *Mitigation strategies*), 30–100 years may be required for MOB communities and total methane flux to recover through afforestation. Careful consideration with regard to the rotation of afforestation, that is, reforestation, field burning and conversion to agricultural soils, should be employed to ensure that soils are maintained as an effective methane sink.

#### Burning of agricultural residues

The burning of agricultural residues contributes marginally to total methane emissions in Australia (0.2–0.3% year<sup>-1</sup> between 1990 and 2011) (Table 1). This practice is typically performed to facilitate planting through the removal of waste plant biomass, to control pests and weeds, and to provide a source of fertilisation through ash (McCarty 2011). An alternative practice that sequesters soil C, improves crop productivity and does not appear to lead to methane emissions is crop stubble retention (Howden and O’Leary 1997; Wang *et al.* 2004; Wang *et al.* 2011; Robertson and Nash 2013). Despite these benefits, occasional burning may be preferable under certain circumstances when managing pests, weeds and disease in no-till management practices and when handling robust stubble from certain crops, such as canola (Ugalde *et al.* 2007).

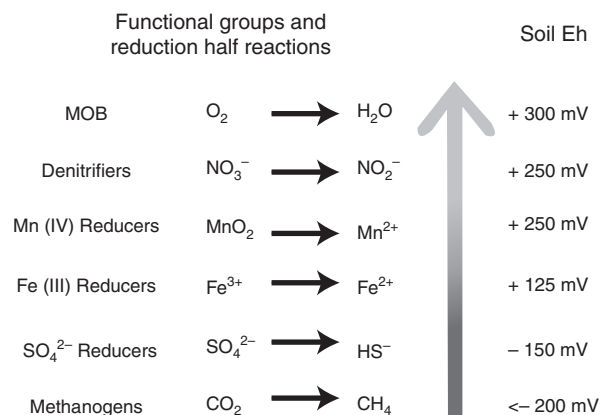
#### Rice cultivation

Rice production in Australia fluctuates depending on water availability, with an average land use of 95 500 ± 51 000 ha between 1990 and 2013 (ABARES 2013). As of 2012–13, 114 000 ha was being used for rice production (ABARES 2013). Unlike cropping and pasture soils, rice cultivation acts as a net methane source due to long-term periods of anoxia in flooded soils. However, rice is cultivated to a small extent in Australia, and accounts for <1% of national annual methane emissions (Table 1). Although this national total is small, these agroecosystems can produce 40–408 kg methane-C ha<sup>-1</sup> season<sup>-1</sup> and are thus important contributors to methane emissions on a local scale (Naser *et al.* 2007; Ly *et al.* 2013). Several factors affect methane flux from rice agroecosystems, such as: (i) soil redox potential (Eh); (ii) temperature;

(iii) plant–microbe and rice cultivar interactions; and (iv) water management, which is discussed as a mitigation strategy (Conrad 2002).

#### Soil Eh

Rice is cultivated in soils that are submerged for a growing season of ~5 months (Humphreys *et al.* 2006). This allows for reduced, anoxic conditions to develop in flooded soils, and the process of microbial anaerobic fermentation, including methanogenesis becomes active. It has been demonstrated that methanogens survive desiccation in rice paddy soil before flooding, and methanogenesis can commence immediately upon inundation (Peter Mayer and Conrad 1990; Yao and Conrad 1999). Acetoclastic and hydrogenotrophic methanogens predominate in rice paddy soils (Conrad 1999; Angel *et al.* 2012; Scavino *et al.* 2013). The substrates for these pathways (acetate, carbon dioxide, carbon monoxide, formate and hydrogen gas) can be utilised by chemoorganotrophs or chemolithoautotrophs, depending upon the availability and Eh of electron acceptors (Le Mer and Roger 2001; Dubey 2005). Competition for these substrates limits methanogenesis, thus reducing total methane emissions. Figure 3 depicts the optimal soil Eh of several microbial functional groups present in rice paddy soils that are either directly involved in methane cycling (MOB, methanogens) or indirectly involved through the competition for substrates with methanogens (adapted from Dubey 2005). It is important to note that methanogenesis is only active under highly reduced conditions (Eh of less than –200 mV). An excellent example of competition between iron(III) reducers and methanogens was documented by Krüger *et al.* (2001), in which acetate produced by microbial fermentation was utilised by iron(III)-reducing bacteria rather than acetoclastic methanogens, and total methane emissions were decreased. Sulfate and nitrate can be important electron acceptors in rice paddy soils, but it is iron(III) that is typically more abundant (Frenzel *et al.* 1999; Yao and Conrad 1999). In Australia, rice is predominantly produced in southern New South Wales (NSW), in the Murrumbidgee,



**Fig. 3.** Optimal soil Eh and reduction half reactions of microbial functional groups involved directly or indirectly in methane production in rice paddy soils. Reducing agents include organic substrates such as formate, acetate, methane, methanol and methylated amines. Adapted from Dubey (2005).



Coleambally and Murray Valley Irrigation Areas (Van Niel and McVicar 2004). A close examination of the concentrations of iron (III), sulfate and nitrate in these rice paddy soils may identify how soil Eh can be used as a potential mitigation strategy under Australian environmental conditions.

#### Temperature

As described previously (*Cropping and pasture soils: Temperature*), temperature has a significant effect on the rate of methanogenesis, the structure of the methanogenic community and production of methanogenic substrates (Wu and Conrad 2001; Conrad 2002). At 30°C and below, acetoclastic methanogenesis predominates in rice paddy soils, although with increasing temperature, hydrogenotrophic methanogenesis begins to become more favourable, and at 50°C virtually all methane is produced by hydrogenotrophs (Conrad 1999; Wu *et al.* 2002). As stated above, hydrogenotrophic methanogenesis can lead to increases in methane emissions to support ATP production (Conrad and Wetter 1990; Thauer *et al.* 2008). Furthermore, the activity of mesophilic MOB decreases at temperatures >30°C and this contributes to total methane flux. In southern NSW, rice is cultivated over the summer period, between October and March, because rice production is sensitive to low temperatures (Humphreys *et al.* 2006). Ambient air temperatures in this region over this period range between 17°C and 36°C (Farrell *et al.* 2006; Matsui *et al.* 2007; Pasuquin *et al.* 2013). It should also be noted that temperature is involved indirectly with additional factors such as soil depth and the production of root exudates by rice plants, and these contribute to changes in the activity of specific methanogen species and total methane emissions (Schütz *et al.* 1990). The upper range of temperatures observed in Australia's predominant rice-growing region is likely to favour the activity of methanogens over methanotrophs; however, studies comparing the activity between these functional groups in Australian agroecosystems need to be conducted to confirm this.

#### Plant-microbe and rice cultivar interactions

Depending on the stage of the growing season, methane emission rates increase as plants develop over time and stimulate rhizosphere microbial communities, and a switch from soil methanogenesis to rhizosphere methanogenesis can be observed (Schütz *et al.* 1989; Ma *et al.* 2012). There are >80 000 rice cultivars in existence, with variable genotypes and phenotypes (Wassmann and Aulakh 2000; Jia *et al.* 2002). In addition to the developmental stage of the plant, the rice cultivar affects both the MOB and methanogen rhizosphere community and their activity, which influences total methane flux from rice agroecosystems (Wu *et al.* 2009; Lüke *et al.* 2011; Gutierrez *et al.* 2013; Han *et al.* 2013). Rice cultivars can differ phenotypically with regard to root biomass, chemical composition and quantity of root C exudates. This affects both oxygen transport to allow for oxidative processes such as methane oxidation or iron(II) oxidation and the supply of C substrates for microbial fermentation (Neue 1993; Watanabe and Kimura 1998; Watanabe *et al.* 1999; Conrad 2002). Significant correlations between root-exudated C and methane

emissions have been noted between cultivars; for example, high dry-matter producing Dular cultivars emitted ~2 mg methane-C plant<sup>-1</sup> h<sup>-1</sup> compared with low dry-matter producing IR65598 cultivars emitting ~0.5 mg methane-C plant<sup>-1</sup> h<sup>-1</sup> 12 weeks post-planting (Wang *et al.* 1997). In addition to root exudates, the vascular transport of methane and oxygen through rice aerenchyma plays a critical role in total methane flux. Indeed, >90% of observed methane emissions from rice agroecosystems occur through rice aerenchyma as MOB consume most methane in paddy soils before its release to the atmosphere (Holzapfel-Pschorn *et al.* 1985; Holzapfel-Pschorn and Seiler 1986). Rice cultivars with increased gas-transport capacity have been shown to emit greater quantities of methane than cultivars with poorer gas-transport capacity (ButterbachBahl *et al.* 1997). This depends on the relative pore diameter of aerenchyma at the root-shoot transition zone (ButterbachBahl *et al.* 1997). The majority of rice cultivated in Australia belongs to temperate Japonica varieties, which include cultivars such as Amaroo, Millin and Calrose (Humphreys *et al.* 2006). Analyses comparing the physiology and methane flux potential of these rice cultivars under Australian environmental conditions should be conducted to evaluate whether specific rice cultivars may have lower gas transport capacity and reduced stimulation of methanogenesis by root exudates.

#### Mitigation strategies

One of the most effective means to reduce methane emissions from rice agroecosystems is through water management. Such regimes can be summarised as continuously flooded, non-flooding irrigated, rain-fed and intermittently flooded (Sanchis *et al.* 2012). Of these, continuously flooded regimes emit significantly greater quantities of methane than the other practices, with short-term, intermittent drainage of soils capable of significantly reducing total methane emissions (Yagi *et al.* 1996; Sanchis *et al.* 2012). Water drainage stops the transcription of genes involved in methanogenesis but does not decrease gene abundance, demonstrating that although methanogenesis is inhibited, aerotolerant methanogens remain present in the soil (Ma and Lu 2011; Scavino *et al.* 2013). The timing of drainage of rice paddy soil is crucial, with midseason aeration of soils most effective at reducing methane emissions without affecting crop production, most likely due to the inhibition of plant-stimulated methanogenesis in the rhizosphere (Ma *et al.* 2013). The effects of midseason drainage are more persistent, with early-stage drainage inhibition persisting for <3 days, whereas midseason drainage effects can persist for >3 weeks (Sigren *et al.* 1997). A drainage period of 48 h is sufficient for long-term methanogenesis inhibition (Ratering and Conrad 1998). The mechanism behind methanogenesis inhibition by short-term water drainage is due to the re-oxidation of electron acceptors such as iron(III) and sulfate, which increases the soil Eh above the ideal conditions for methanogenesis (Sigren *et al.* 1997; Ratering and Conrad 1998). This is dependent upon the Eh potential of the rice paddy soil. The addition of ferric iron oxide or nitrate to rice paddy soils increases soil Eh and inhibits methanogenesis, but may have detrimental effects on

crops or lead to the emission of nitrous oxide, depending on the concentration of amendments (Klüber and Conrad 1998; Jäckel and Schnell 2000). Unfortunately, midseason water drainage may not be a viable mitigation strategy in Australian rice agroecosystems because this practice relies on water availability, which is a frequent concern for Australian rice farmers (Humphreys *et al.* 2006; Sanchis *et al.* 2012).

The addition of rice straw, nitrate or ammonium as a fertiliser can lead to complex responses from both MOB and methanogens. The fermentation of rice straw leads to increased methane emission from rice paddies (Sanchis *et al.* 2012). If rice straw is to be used as a fertiliser, it should be applied during the fallow season (Yan *et al.* 2009). As described above in *Ammonium and nitrate availability*, nitrate and ammonium addition can lead to inconsistent results in relation to methane flux because of the curvilinear relationship between concentration and MOB and/or methanogen activity (Banger *et al.* 2012; Pittelkow *et al.* 2013). The efficient use of 140–200 kg N ha<sup>-1</sup> has been shown to maximise crop yield in relation to total annual global water potential (Pittelkow *et al.* 2013). Improvements in water use efficiency, soil Eh, cultivar root-C exudates, cultivar methane vascular transport, and fertilisation amendments should all be considered when trying to mitigate methane emissions from Australian rice agroecosystems.

### Enteric fermentation and manure

Enteric fermentation by ruminant livestock is the greatest anthropogenic source of methane in Australia, contributing 52.4% of emissions (2.83 Mt methane year<sup>-1</sup>) between 1990 and 2011 (Table 1). In Australia, methane emissions from enteric fermentation are determined by livestock populations, with dairy cattle emitting 250–430 g methane day<sup>-1</sup>, beef cattle 240–350 g methane day<sup>-1</sup> and adult sheep 22–25 g methane day<sup>-1</sup> (Cottle *et al.* 2011). Between 2000 and 2011, average livestock populations were roughly 3 million dairy cattle, 25 million beef cattle and 92 million adult sheep (ABARES 2011). Manure contributes considerably less methane, accounting for 1.6% of emissions (84.4 kt methane year<sup>-1</sup>) between 1990 and 2011 (Table 1).

### Microbial fermentation in the rumen

Ruminant animals have coevolved with a complex gut microbiota in a manner that has mutualistically improved the efficiency of digestion of complex plant polymers (Hungate 1988). In ruminants, microbial fermentation primarily occurs in the pre-gastric reticulum and rumen, where fluid mixes freely through the reticulo-rumen fold in adult ruminants (Church 1976). The development of a multi-chambered fore-stomach allows for increased retention time of ingested plant biomass and therefore a greater degree of microbial fermentation of non-labile C in the form of lignin, cellulose and hemicellulose (Hungate 1988; McSweeney and Mackie 2012).

A vast array of functionally diverse anaerobic microorganisms inhabits the rumen, and their role in fermentation has been reviewed extensively elsewhere (Krause *et al.* 2003; Edwards *et al.* 2008; Kim *et al.* 2011; McSweeney and Mackie 2012). Of particular importance are organisms involved in cellulose,

hemicellulose, cellobiose, xylan, lipid and protein metabolism (Nugent and Mangan 1981; Mackie and Kistner 1985; Jenkins 1993; Hess *et al.* 2011). Most of these organisms are closely associated with particulate plant biomass and other microflora to facilitate syntrophic interactions such as plant biomass degradation and interspecies electron transfer (McAllister *et al.* 1996; Edwards *et al.* 2008; Leng 2014). The final products of enteric fermentation include acetate, formate, methanol, carbon monoxide, carbon dioxide and hydrogen gas, all of which are substrates for methanogenesis. Methane measurements have shown that the rumen is the primary site of enteric fermentation, with 87% of methane produced in the rumen, and up to 13% produced in the lower digestive tract (Murray *et al.* 1976). Most of methane is eructated by the animal or absorbed into the blood stream and exhaled via the lungs, with a small proportion (1–2%) expelled as flatulence (Murray *et al.* 1976). Methane constitutes ~10% of expelled gas, although this is diet-dependent (Ding *et al.* 2010; Madsen *et al.* 2010).

A primary factor for enteric methane production is dietary carbohydrate, which influences the rate of fermentation, rate of rumen passage, and animal intake (Johnson and Johnson 1995). The digestibility of ingested plant biomass, which is determined by the ratio of insoluble cell wall fibre to soluble carbohydrates, directs enteric fermentation to the preferential production of certain end products (Egan 1989; Jung *et al.* 1993; Migwi *et al.* 2013). Highly fibrous, poorly digestible plant biomass leads to the production of higher proportions of methanogenic substrates and reduces rumen passage rates, resulting in higher rates of methane production (Moe and Tyrell 1975; Beever *et al.* 1989; Alford *et al.* 2006; Ellis *et al.* 2008).

Australian rangelands utilised for livestock grazing are highly variable and cover diverse grassland or shrubland ecosystems from arid and semi-arid southern and western regions of Australia to tropical woodlands in northern Australia (McKeon *et al.* 2004). High fibre, low protein, poorly digestible C<sub>4</sub> forages are most common in the northern tropics and subtropics (Leng 1990; McKeon *et al.* 2004; Bastin 2008; Devendra and Leng 2011). Temperate C<sub>3</sub> forages, such as those in south-eastern Australia, are typically considered to have a higher average digestibility (Fahey and Hussein 1999; McKeon *et al.* 2004; Bastin 2008). Between 2009 and 2011, livestock densities have simultaneously increased in northern Australia and decreased in southern Australia (Bastin 2011). Depending on farm-scale management, this has implications for agricultural methane emissions, because 10–17% more methane is produced from the fermentation of C<sub>4</sub> plant biomass than C<sub>3</sub> plant biomass (Ulyatt *et al.* 2002; Beauchemin *et al.* 2008; Archimède *et al.* 2011).

### Rumen methanogens

Methanogens form a large portion of the rumen microbiota, present at >10<sup>6</sup> cells mL<sup>-1</sup> rumen contents (Bryant 1970). Representatives from the following orders of methanogens have been identified in rumen microbial communities: Methanococcales, Methanobacteriales, Methanomicrobiales, Methanosarcinales and Thermoplasmatales (Tajima *et al.* 2001;

Nicholson *et al.* 2007; Janssen and Kirs 2008; Poulsen *et al.* 2013). Enteric fermentation is thermodynamically favourable only when a hydrogen sink is present and the major hydrogen-utilising microorganisms in the rumen are hydrogenotrophic methanogens (Lin *et al.* 1997). Hydrogenotrophic species belonging to the genus *Methanobrevibacter* are frequently the most active and abundant methanogens in the rumen of cattle and sheep (Nelson *et al.* 2003; Wright *et al.* 2008). Sequencing of the genome of the type strain *Methanobrevibacter ruminantium* M1 has provided several insights into the ecology of a widespread rumen methanogen (Leahy *et al.* 2010). These include an unusually high number of adhesion-like proteins encoded by the genome compared with other gut methanogens, auxotrophic for the synthesis of coenzyme M, an essential co-factor for methanogenesis, and the lack of methyl coenzyme reductase II, which is necessary for methanogenesis in the presence of high partial pressures of hydrogen (Leahy *et al.* 2010). All of these support a requirement for close syntrophic associations between hydrogenotrophic methanogens and other rumen microflora.

Acetoclastic and methylotrophic methanogens such as *Methanosarcina*, *Thermoplasmata* and *Methanospaera* spp. have also been identified from the rumen; however, these metabolic pathways are either less thermodynamically favourable in the rumen (acetoclastic) or limited by substrate availability (methylotrophic) (Liu and Whitman 2008). The structure of the rumen microbiome is affected by diet, host genetics, acquisition at birth, seasonal and geographic factors (Kim *et al.* 2011). It has been noted that under certain conditions methylotrophic methanogens can be the predominant species present, and these organisms produce greater quantities of methane than hydrogenotrophic methanogens (McSweeney and Mackie 2012). Although this is unusual, it does emphasise the plastic nature of the rumen microbiome and suggests the potential for management strategies to limit enteric methane production.

#### Mitigation strategies for enteric fermentation

Enteric fermentation is a dominant source of anthropogenic methane, and therefore, mitigation strategies have been the focus of several recent reviews (Beauchemin *et al.* 2008; McAllister and Newbold 2008; Eckard *et al.* 2010; Hegarty *et al.* 2010; Cottle *et al.* 2011). The most successful mitigation strategies have revolved around dietary manipulation to reduce methane production per unit liveweight gain. In feedlot systems, concentrate supplementation and/or grain finishing diets have been shown to reduce methane emissions and improve animal productivity (Beauchemin and McGinn 2005). Lipid supplementation can reduce methanogenesis without negatively affecting total digestibility, although this is concentration-dependent (Hook *et al.* 2010; Patra 2014). The microbial efficiency of fibre digestion can be improved through urea or protein supplementation, which improves rumen passage rates and reduces total methane emissions (Patra 2012). An additional approach to improving rumen passage rates is by reducing the surface area to volume ratio of feed (Johnson and Johnson 1995; Ellis *et al.* 2008). If local environmental conditions allow, methane emissions can be

reduced by improving feed digestibility through the modification of grazing pastures (C<sub>3</sub> v. C<sub>4</sub> forages) or the selection of plant species that produce secondary metabolites to reduce methanogenesis, such as saponins, flavonoids and tannins (Abberton *et al.* 2007; Dewhurst *et al.* 2009; Clark *et al.* 2011).

Animal traits that affect methane production, and which can be selectively bred for, include feed utilisation efficiency, residual feed intake, methane production per unit dry matter intake, and the rumen microbiota itself (Alford *et al.* 2006; Hegarty *et al.* 2010; Basarab *et al.* 2013). Cattle bred for increased efficiency have been demonstrated to have markedly different methanogen communities and fewer organisms involved in benzoic acid metabolism, which has implications for the production of methanogenic substrates (Zhou *et al.* 2009; Goshal *et al.* 2012). Breeding to improve these factors is likely to be an ideal means towards further mitigation of methane production because it has the potential to compliment dietary management strategies in that they improve animal liveweight gain per unit methane produced (Eckard *et al.* 2010).

Another method involves anti-methanogenic treatments, such as the addition of halogenated methane analogues to the diet (Zinder *et al.* 1984; Denman *et al.* 2007b; Goel *et al.* 2009), anti-methanogenic plant secondary metabolites (Bodas *et al.* 2008), anti-microbial bacteriocins (Klieve and Hegarty 1999), vaccines targeting antigens specific to methanogens (Wright *et al.* 2004), and defaunation of the rumen to remove syntrophic hydrogen-producing protozoa (Hook *et al.* 2010).

Finally, the introduction of organisms that function as competitive hydrogen sinks has received much attention, including reductive acetogens (Morvan *et al.* 1996; Lopez *et al.* 1999), sulfate-, nitrate- and fumarate-reducing bacteria (McAllister *et al.* 1996; Asanuma and Hino 2000; McGinn *et al.* 2004), and organisms involved in biohydrogenation of unsaturated fatty acids (Harfoot 1978).

#### Manure and manure management strategies

Ingested plant biomass is not completely fermented within the rumen, as demonstrated by the continuation of fermentation, and methanogenesis, within animal manure (Sorlini *et al.* 1988). Complications from manure management arise when manure is allowed to accumulate and anoxic conditions suitable for methanogen activity arise (Philippe *et al.* 2007). The primary drivers of methanogenesis in stored manure are: the time of storage, the means of storage including manure covers, and temperature (Monteny *et al.* 2006; Chianese *et al.* 2009; Montes *et al.* 2013). These factors affect the onset of anoxia and the rate of methanogenesis.

Manure is a valuable fertiliser resource and improves soil organic matter, soil microbial biomass, and water-holding capacity, and contributes to increases in crop yields while decreasing soil erosion (Montes *et al.* 2013). As mentioned above in *Mitigation strategies*, organic fertilisers are a preferable alternative to synthetic fertilisers, because they do not inhibit soil methane uptake (Skinner *et al.* 2014). However, manure application can lead to nutrient build-up, potential loss of N and phosphorus to the environment, eutrophication of



water sources, and GHG emissions if applied in quantities that exceed the soil's retention capacity (Saam *et al.* 2005). Another use for manure that generates energy and mitigates methane emissions is the use of anaerobic digesters or gas-impermeable covers to capture biogas (which consists of 60–80% methane), with subsequent incineration for energy generation (Prapasongsa *et al.* 2010; Rotz *et al.* 2011). This approach requires additional inputs in the form of industrial- or plant-waste biomass because methanogenesis from manure alone may not produce sufficient quantities of methane (Prapasongsa *et al.* 2010). For smaller scale farms (herds of 100–350 animals), a more cost-effective means to reduce methane emissions may be via the use of biofilters, which filter methane from an anaerobic source and oxygen through an artificial soil MOB community (Melse and Van der Werf 2005; Pratt *et al.* 2012). The implementation of such mitigation strategies depends largely on construction and energy costs, and government incentives for investment in renewable energy technology (Wilkinson 2011).

### Climate-change factors affecting methane sources, sinks and mitigation

Total atmospheric methane concentrations shifted from 380 ppb during the last glacial maximum to 715 ppb during pre-industrial times due to the effect of local climatic factors on the strength of natural sources and sinks of methane (O'Connor *et al.* 2010). This is primarily a consequence of changes in feedback mechanisms for total methane flux, such as temperature (O'Connor *et al.* 2010). As the global climate continues to change over the next century, several predictions relevant to methane cycling in Australian agroecosystems have been made. These include: increases in the frequency, duration and magnitude of hot extremes, increases in evapotranspiration and subsequent decreases in soil moisture, increases in the frequency and intensity of heavy rainfall events with a simultaneous decrease in total average precipitation, increases in the frequency of naturally occurring wild fires, increases in atmospheric carbon dioxide concentrations, and decreases in average vegetation cover (Meehl and Stocker 2007; Pitman *et al.* 2007; Pitman and Perkins 2008; Baldock *et al.* 2012; Pery *et al.* 2012; Collins *et al.* 2013). These variables may contribute to positive feedback (e.g. increased rates of microbial activity) or negative feedback (e.g. decreased total microbial biomass and/or biodiversity) on regional scales, and predicting how microorganisms will respond to climate change is particularly daunting (Singh *et al.* 2010).

Increases in ambient temperature, decreases in soil moisture (arid to very arid) and decreases in vegetation are likely to have a negative effect the activity of atmospheric methane oxidation by MOB. In Australian pasture and cropping soils, this could act as a positive feedback mechanism and contribute to increasing atmospheric methane concentrations and global mean surface temperatures. Furthermore, an increase in high-intensity rainfall events and flooding will temporarily alter these agroecosystems from net methane sinks to net methane sources depending on the soil Eh and duration of flooding (Otter and Scholes 2000). Elevated carbon dioxide concentrations may lead to

improved soil moisture in the rhizosphere because of increased root exudation, but how this will affect the biodiversity and activity of soil MOB communities in semi-arid soils is uncertain (Dijkstra *et al.* 2011). In temperate soils where soil moisture may not be limiting, elevated carbon dioxide concentrations and temperatures have been shown to decrease MOB activity, either indirectly through increased soil moisture in the rhizosphere or by directly affecting the MOB community (Phillips *et al.* 2001; McLain and Ahmann 2008).

It is expected that the frequency of naturally occurring fires will increase as a result of climate change (Pitman *et al.* 2007; Pitman and Perkins 2008), and although this may increase direct emissions of GHGs, the long-term effects of fire on soil MOB activity may not be negative. Research into the short- and long-term effects of fires with concurrent increases in temperature and decreases in soil moisture will need to be conducted to evaluate how MOB soil communities will respond.

In Australian rice agroecosystems, increasing ambient temperatures predicted as a consequence of global climate change are likely to increase overall anaerobic respiration and methanogen activity and may limit MOB activity. A study investigating the impacts of elevated carbon dioxide on rice soils demonstrated significant increases in methane emissions (Dijkstra *et al.* 2010). This may be a consequence of changes in root exudation rates and rhizosphere–methanogen interactions. Unfortunately, because water management is a limitation for rice farmers in Australia (Humphreys *et al.* 2006; Sanchis *et al.* 2012) and drought frequency is expected to increase, midseason drainage as a mitigation strategy for methane emissions may become less viable.

In grazing livestock production systems, animal density and forage biomass are intrinsically linked to rainfall patterns (McKeon *et al.* 2004; Bastin 2011; Migwi *et al.* 2013). With decreases in total average precipitation and vegetation cover predicted, livestock populations and enteric methane emissions are likely to decrease as well. However, because heat stress increases the production of lignin in plant biomass, it is possible that increases in global temperatures, particularly in the tropics, will decrease the overall digestibility of forages while also increasing enteric methane production, and this will have negative implications for methane production per unit liveweight gain (Buxton and Fales 1994; Fahey and Hussein 1999; Migwi *et al.* 2013). Further work to quantify the simultaneous effects of multiple climate drivers on methane flux in Australian agroecosystems must be conducted to understand how terrestrial methane budgets are likely to change over time.

### Conclusion

Global atmospheric methane concentrations are increasing because of greater rates of production compared with removal. In Australia, agriculture represents an important source for anthropogenic methane emissions, whereas cropping and grazing soils may represent Australia's largest potential terrestrial methane sink due to extensive land area. Methanogenic and methanotrophic microbial functional groups

play an important role in total methane flux from agroecosystems. The factors that regulate the activity of these organisms (temperature, soil moisture, ammonium, nitrate, land-use management, soil pH, soil Eh, C substrates, and plant– and animal–microbe interactions) have been well documented. These studies have led to a variety of mitigation strategies for the reduction of methane emissions from agroecosystems. Effective implementation of these strategies, such as no-till management and crop stubble retention, depend on cost, effects on crop and livestock production, and government policy. Importantly, there remains some uncertainty as to the extent of atmospheric methane oxidation in Australian cropping and pasture soils. Accurate modelling and prediction of the role of these soils in balancing Australia's methane budget would assist in defining policy goals with regard to land use and GHG mitigation. Future research should focus on assessing the role of these soils in Australia's methane budget, linking the biodiversity and activity of methanogens and MOB to environmental factors, and quantitatively investigating how a combination of climate change drivers is likely to affect production and oxidation of methane in these agroecosystems.

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