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Review

Essential oils in poultry nutrition: Main effects and modes of action

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ABSTRACT

Antimicrobial compounds produced by microorganisms have been used for decades in poultry diets to increase performance and decrease morbidity particularly in broiler chickens. However, consumer pressure related to the potential development of antibiotic-resistant bacteria has resulted in the development of non-antibiotic feed additives that may also improve broiler performance. In recent years, aromatic plants and their extracts have received attention as growth and health promoters. It is known that most of their properties are due to the essential oils (EOs) and other secondary plant metabolites. EOs enhance production of digestive secretions, stimulate blood circulation, exert antioxidant properties, reduce levels of pathogenic bacteria and may enhance immune status. The purpose of this paper is to provide an overview of the published data on the potential of EOs and their components in poultry nutrition, and to describe their possible modes of action. The current knowledge on potential antagonistic and synergistic effects is presented and areas for future research are proposed.

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Abbreviations: ADG, average daily gain; AGP, antibiotic growth promoters; ATP, adenosine triphosphate; EOs, essential oils; BHA, butylated hydroxyanisole; BHT, butilated hydroxytoluene; BW, body weight; GI, gastrointestinal tract; LD50, lethal dose 50; MIC, minimum inhibitory concentration; TRP, transient receptor potential; TRPV1, transient receptor potential vanilloid type; TRPA1, transient receptor potential ankyrin type; TRPM4, transient receptor potential melastatin type.

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1. Introduction

The prophylactic use of antibiotics in poultry nutrition to cause improvements in growth, feed consumption, feed utilization and decreased mortality from clinical diseases is well documented. However, the growing concern over the transmission and the proliferation of resistant bacteria via the food chain has led to a ban of the feed use of antibiotic growth promoters (AGP) in livestock within the European Union since 2006. As a result, new commercial additives derived from plants including aromatic plant extracts and their purified constituents have been examinated as part of alternative feed strategies for the future. Such products have several advantages over commonly used commercial antibiotics since they are residue free and they are also, generally recognized as safe and commonly used items in the food industry (Varel, 2002). These botanicals have received increased attention as possible growth performance enhancers for animals in the last decade. The market for plant-based performance enhancers has increased since the 1990s. For example sales for EOs in the EU reached 90 t in 1996 while the forecast only ten years later was of 600 t (Greathead, 2003).

The EOs -also called volatile or ethereal oils- are aromatic oily liquids obtained from plant material (flowers, buds, seeds, leaves, twigs, bark, herbs, wood, fruits, and roots). EOs are complex mixtures of secondary plant metabolites consisting of low-boiling-phenylpropenes and terpenes. They are particularly associated with characteristic plant essences and fragrances, the *quinta essentia*, defined as "herbs and spices". They are typically extracted by distillation methods, in particular steam distillation (Greathead, 2003). An estimated 3000 EOs are known, of which about 300 are commercially important and are used mainly in the flavours and fragrances market (Van de Braak and Leijten, 1999). Apart from their traditional use, a host of beneficial effects have been reported by experimental studies during the past three decades. Among these are their beneficial influence on lipid metabolism, ability to stimulate digestion, antimicrobial and antioxidant properties, and anti-inflammatory potential (Acamovic and Brooker, 2005).

The EOs and various extracts of plants have increased in appeal since they are aligned with current thinking on the future of agriculture in the EU, and with consumer preference for natural products. Moreover, their beneficial attributes have the potential of a possible therapeutic exploitation in a variety of conditions. The antimicrobial properties of EOs have been widely reported (Dorman and Deans, 2000; Mourey and Canillac, 2002; Rota et al., 2004). In fact, given their antimicrobial properties, EOs have been applied as potential feed additives (Nychas, 1995; Tuley de Silva, 1996; Lee et al., 2004). Besides antibacterial properties, EOs or their components have been shown to exhibit hypolipidemic (Srinivasan, 2004), antioxidant (Kempaiah and Srinivasan, 2002; Botsoglou et al., 2004), digestive stimulant (Platel and Srinivasan, 2004), antiviral (Bishop, 1995), antimycotic (Jayashree and Subramanyam, 1999; Mari et al., 2003), antitoxigenic (Ultee and Smid, 2001; Juglal et al., 2002), antiparasitic (Pandey et al., 2000; Pessoa et al., 2002), and insecticidal (Konstantopoulou et al., 1992; Karpouhtsis et al., 1998) properties as well as inhibition of odour and ammonia control (Varel, 2002). These characteristics are possibly related to the function of these compounds in plants (Mahmoud and Croteau, 2002). In contrast, many herbs and spices are popular food condiments. EOs and oleoresins of garlic and capsicum as well as cinnamic aldehyde, carvacrol and pipperine (from black pepper) among others, have long been used due to their food flavor enhancement properties. Some researchers have found that many herbs and botanicals are able to improve growth rate through increased feed intake (Wenk, 2006), nevertheless, others have reviewed the topic and found no clear evidence that herbs and spices improve palatability in farm animals (Windisch et al., 2008).

The purpose of this paper is to provide an overview of the published data on the potential of EOs and their components in poultry nutrition, and to describe their possible modes of action. The current knowledge on potential antagonistic and synergistic effects is presented and areas for future research are proposed.

2. Composition of EOS

Detailed compositional analysis of volatile compounds is performed by gas chromatography and mass spectrometry of the EO (Daferera et al., 2000; Juliano et al., 2000; Jerkovic et al., 2001; Delaquis et al., 2002). EOs, from the chemical point of view, are quite complex mixtures constituted by several dozens of components, and this complexity makes it often difficult to explain their activities (Senatore, 1996; Russo et al., 1998). They are variable mixtures of mainly terpenoids (linalool, geraniol, thujanol, borneol, menthol, citronnillol, α-terpineol), and a variety of low molecular weight aliphatic hydrocarbons (e.g. phenols as thymol, carvacrol, eugenol, gaiacol, and aromatic aldehydes as cinnamaldehyde, cuminal and phellandral) (Dorman and Deans, 2000). Major components are characterized by two or three components at fairly high concentrations (up to 85%) compared to others components present in trace amounts (Senatore, 1996; Bauer et al., 2001). Generally, the main constituents reflect the biophysical and biological features of the EOs from which they were isolated. The phenolic components are primarily responsible for the antibacterial properties of EOs (Cosentino et al., 1999).

The major components of a number of EOs, according to Chao et al. (2000), are presented in Table 1. These components have either been shown to have antibacterial activity and the data on their mode of action are discussed in this paper. There is some evidence that the activity of the main components is modulated by other minor molecules. Some studies have concluded that whole EOs have a greater antibacterial activity than the major components mixed (Gill et al., 2002; Mourey and Canillac, 2002), which suggests that the minor components are critical to the activity and may have a synergistic effect or potentiating influence. This has been found to be the case for sage (Marino et al., 2001), certain species of *Thymus* (Lattaoui and Tantaoui-Elaraki, 1994; Paster et al., 1995; Marino et al., 1999) and oregano (Paster et al., 1995).

Table 1
Some essential oils and their major components (Chao et al., 2000).

Essential oil	Main components	Total (%)	Essential oil	Main components	Total (%)
Angelica root	α-Pinene	24.7	Mandarine	Limonene	79.5
	δ-3-carene	10.5		γ-Terpinene	9.7
	α-Phellandrene + myrcene	10.8			
	Limonene	12.9			
	β-Phellandrene	10.4			
	ρ-Cymene	7.7			
Bergamot	β-Pinene	7.7	Nutmeg	α-pinene	26.0
	Limonene + β-phellandrene	39.4		β-pinene	15.0
	γ-Terpinene	8.6		Sabinene	27.1
	Linalool	11.1		Myristicin	5.9
	Lynalil acetate	28.0			
Cynnamon bark	(E)-Cinnamaldehide	77.1	Orange	Limonene	91.5
	Eugenol	7.2			
Coryander	ρ-Cymene	6.1	Pepper	α-Pinene	9.0
	Linalool	72.0		β-Pinene	10.4
				Sabinene	19.4
				δ-3-Carene	5.4
				Limonene	17.5
				β-Caryophyllene	14.7
Dill (Indian)	Limonene	50.9	Pine (Scotch)	α-Pinene	9.0
	Trans-Dihydrocarvone	10.4		β-Pinene	10.4
	Carvone	20.3		δ-3-carene	21.6
	Dillapiole	36.3		Myrcene + α-terpin	5.8
Eucalyptus	Citronellal	72.8	Rosemary	α-Pinene	7.4
	Citronellol	14.5		β-Pinene	5.0
				1,8-Cineole	43.6
				Camphor	12.3
Geranium	Isomenthone	6.4	Rosewood	Linalool	80.0
	Citronellol	42.0			
	Geraniol	5.5			
	Cytronellyl formate	14.2			
Ginger	Camphene	14.1	Sage	1,8-Cineole	8.4
	Neral	4.9		α-Thujone	31.8
	Geranial + bornyl acetate	8.1		β-Thujone	33.2
	β-Bisabolene	22.1			
	Ar-Curcumene	14.5			
	β-Eudesmol	5.4			
Juniper berry	α-Pinene	33.7	Savory	γ-Terpinene	7.4
	Sabinene	27.6		ρ-Cymene	25.9
	Myrcene	5.5		Carvacrol	37.7
Lime	Geranial	6.0	Tarragon	(Z)-β-Ocimene	7.3
	Limonene	55.5		(E)-β-Ocimene	6.9
	β-Pinene	11.0		Methyl chavicol	77.6
	γ-Terpinene	14.5			

Due to their natural origin, environmental and genetic factors will influence the chemical composition of the plant EOs. Factors such as species and subspecies, geographical location, harvest time, plant part used and method of isolation all affect chemical composition of the crude material separated from the plant (Cosentino et al., 1999; Marino et al., 1999; Juliano et al., 2000; Faleiro et al., 2002). It was postulated that individual components of EOs exhibit different degrees of antibacterial activity (Dorman and Deans, 2000) and it is known that the chemical composition of EOs from a particular plant species can vary according to the geographical origin and harvesting period. It is therefore possible that variation in composition between batches of EOs is sufficient to cause variability in their biological activity. This can be explained, at least in part, by the formation of active ingredient precursors. *p*-cymene (1-methyl-4-(1-methylethyl)-benzene) and γ-terpinene (1-methyl-4-(1-methylethyl)-1,4-cyclohexadiene) are the precursors of carvacrol (2-methyl-5-(1-methylethyl)phenol) and thymol (5-methyl-2-(1-methylethyl)phenol) in species of *Origanum* and *Thymus* (Cosentino et al., 1999; Jerkovic et al., 2001; Ultee et al., 2002). The season of collection strongly affects the yield of EOs from the plant and the concentration of the two phenol precursors. Despite the striking quantitative differences of the major oil components, the sum of the amounts of these four compounds present in Greek oregano plants has been found to be almost equal in specimens derived from different geographical regions (Kokkini et al., 1997), and to remain stable in plants harvested during different seasons (Jerkovic et al., 2001). The same is true of *Thymus vulgaris* from Italy (Marino et al., 1999). This indicates that the four compounds are

Table 2
Effect of EOs on production performance in poultry (adapted from Windisch et al., 2008).

	Treatment effect, % difference from control					
	Dietary dose (g/kg)	Feed intake	BW	ADG	Feed conversion ratio	Reference
BROILERS						
Plant extracts						
Oregano	0.15	−6		−2	−4	Basmacioglu et al. (2004)
Oregano	0.3	−3		+1	−2	Basmacioglu et al. (2004)
Rosemary	0.15	0		−1	−1	Basmacioglu et al. (2004)
Rosemary	0.3	−2		+1	−4	Basmacioglu et al. (2004)
Thymol	0.1	+1		+1	−1	Lee et al. (2003)
Cinnamon	0.1	−2		−3	0	Lee et al. (2003)
Thymol	0.2	−5		−3	−3	Lee et al. (2003)
Carvacrol	0.2	+2		+2	−1	Lee et al. (2003)
EO blend	0.024	−4	0		−4	Cabuk et al. (2006)
EO blend	0.048	−5	0		−6	Cabuk et al. (2006)
Plant extracts	0.2		−2	0	−2	Hernandez et al. (2004)
Plant extracts	5.0		+2	+3	−4	Hernandez et al. (2004)
Plant extracts	0.5	0	−2	−2	+2	Botsoglou et al. (2004)
Plant extracts	1.0	+2	−1	0	+2	Botsoglou et al. (2004)
EO blend	0.075	−7		−3	−4	Basmacioglu et al. (2004)
EO blend	0.15	−7		−1	−1	Basmacioglu et al. (2004)
EO blend	0.036	+3	−8		−5	Alcicek et al. (2004)
EO blend	0.048	+2	−8		−4	Alcicek et al. (2004)
Plant extracts	0.1	+1		+1	0	Lee et al. (2003)
EO blend	0.024	−2	0		−2	Alcicek et al. (2004)
EO blend	0.048	0	+14		−12	Alcicek et al. (2004)
EO blend	0.072	−2	+8		−9	Alcicek et al. (2004)
Spices						
Oregano	5.0	+5		+7	−2	Florou-Paneri et al. (2006)
Thyme	1.0	+1	+2		−1	Sarica et al. (2005)
Garlic	1.0	−5	−5		0	Sarica et al. (2005)
TURKEYS						
Spices						
Oregano	1.25	−5	+2			Bampidis et al. (2005)
Oregano	2.5	−6	+1			Bampidis et al. (2005)
Oregano	3.75	−9	+1			Bampidis et al. (2005)
QUAIL						
Eos						
Thyme	0.06	0		+6		Denli et al. (2004)
Black seed	0.06	+1		+2		Denli et al. (2004)
Spices						
Coriander	5.0	+3		+1	+1	Güler et al. (2005)
Coriander	10.0	+3		+5	−1	Güler et al. (2005)
Coriander	20.0	+4		+8	−4	Güler et al. (2005)
Coriander	40.0	+5		+4	+1	Güler et al. (2005)

biologically and functionally closely associated and supports the theory that thymol is formed via *p*-cymene from γ-terpinene in *T. vulgaris* (Kokkini et al., 1997). Generally, EOs produced from herbs harvested during or immediately after flowering have the strongest antimicrobial activity (McGympsey et al., 1994; Marino et al., 1999). In fact, the composition of EOs from different parts of the same plant differs widely. For example, EOs obtained from the seeds of coriander (*Coriandrum sativum* L.) has a different composition compared to cilantro, which is obtained from the immature leaves of the same plant (Delaquis et al., 2002). Finally, changes in the potency of the antimicrobial activity have also been related to changes in the enantiomer ratio of active EO components (Lis-Balchin et al., 1996).

3. Use of EOs in poultry diets

There are a limited number of controlled studies on the effect of EO components on growth performance, digestive enzymes activities and macronutrient digestibility in broiler chickens. Variable effects on performance have been reported. A summary of recent publications on the effect of EOs on productive performance parameters have been reported by Windisch et al. (2008). As shown in Table 2, the majority of experimental results indicate reduced feed intake at largely unchanged body weight gain or final body weight, leading to an improved feed conversion ratio when feeding EOs. No influence on performance parameters has been reported by different authors (Botsoglou et al., 2002a; Lee et al., 2003; Hernández et al., 2004; Shanmugavelu et al., 2004; Jang et al., 2007) using oregano essential oil, thymol, cinnamaldehyde, pepper, garlic powder and a commercial blend of EO containing thymol. However, a summary of different research carried out in Europe, illustrating the positive effect on broiler performance of plant extracts (capsaicin and polyphenols) has been published by Kamel (2000, 2001). Similarly, the inclusion of a plant extract containing capsaicin, cinnamaldehyde, and carvacrol (Jamroz et al., 2003), garlic powder (Lewis et al., 2003; Cross et al., 2004), garlic and thymol powder (Demir et al., 2003), and a combination of EOs (Alcicek et al., 2003, 2004) as well as numerous field studies (Bassett, 2000; Langhout, 2000; Kamel, 2001) observed improvements in the performance of broilers and carcass yield and a reduction in the intestinal weight. Demir et al. (2003) attributed this improvement to the significant reduction in the depth of the crypts in the ileum with the inclusion of thyme and garlic. In early maturing turkeys, Bampidis et al. (2005) also showed that dietary oregano leaves improved feed conversion ratio.

The variability in the efficacy of EOs on animal performance could be attributed, among others, to the composition of the basal diet (less digestible diet), level of feed intake, hygienic standards and environmental conditions Other factors that could affect the results of *in vivo* experiments are: harvesting time and state of maturity of plants, extraction methods of plants, method and duration of conservation and storing and possible synergistic or antagonistic effect of the bioactive compounds.

4. Mode of action of EOS in poultry nutrition

Spices, which are used as food additives to enhance the taste and flavour of food, are also believed to exhibit a range of beneficial physiological effects. Following the ban on the use of antibiotics as growth promoters the use of EOs in poultry production is becoming more common. However, the mode of action of the bioactive compounds in birds has not yet been fully explained. Based upon the current avian literature we identified different mechanisms of the EOs actions that we have grouped into four categories: sensorial, metabolic, antioxidant and antimicrobial.

4.1. Sensorial: oronasal sensing and digestive conditioning

The digestive stimulant action is probably the most commonly experienced beneficial physiological effect of spices. Largely empirical knowledge of this attribute has recently been shown in experimental animal studies. EOs and/or oleoresins of garlic, fenugreek, curcumin, onion, mint, black pepper, cinnamon and capsicum among others and their active compounds act as food condiments through the combined activation of the three peripheral sensing mechanisms found in the oral and nasal cavities (from now on referred to as oronasal): somatosensing, smell and taste (Tominaga and Julius, 2000; Platel and Srinivasan, 2004; Srinivasan, 2007). Oronasal sensing prepares the gastrointestinal (GI) tract for food reception and stimulates digestive secretions and gut motility (Ohara et al., 1988; Katschinski, 2000; Teff, 2000; Hiraoka et al., 2003; Laugerette et al., 2005). The somatic sensing in the oronasal cavity is linked to the cranial nerve V (the trigeminal) and covers all the oronasal epithelium and detects touch and proprioception (Aβ-fibers) noxious temperatures (low or high) and chemesthesis (Aδ-fibers) and pain (C-fibers) including pungency by acids and spices (Miller and Teates, 1984; Hyde and Witherly, 1993; Tominaga and Julius, 2000; Djouhri and Lawson, 2004). Noxious, high and low temperatures but also pungent and spicy compounds may lead to mucosal damage in the GI. The trigeminal stimulation consequently leads to an alarm response characterized by feed avoidance (Tewksbury and Nabhan, 2001), followed by an integrated mucous secretory response of the GI tract and an increase in the intestinal motility aimed to protect the digestive epithelium (Kaunitz and Akiba, 2001; Akiba et al., 2002; Platel and Srinivasan, 2004). Spices or their active principles have been reported to stimulate digestive secretions such as saliva (and salivary amylase) in humans and gastric, bile acids, pancreatic enzymes (lipase, amylase and proteases) and intestinal mucosa in rats (Glatzel, 1968; Platel and Srinivasan, 2000a,b, 2001, 2004; Platel et al., 2002).

Temperatures but also pungency or spiciness are perceived through the stimulation of transmembrane ion channels (members of the transient receptor potential family—TRP-) mainly the heat activated vanilloid (TRPV1-4) and melastatin (TRPM2,4,5) types and the cold activated ankyrin family (TRPA1) and the melastatin family member 8 (TRPM8) present in the neurons of the trigeminal nerve fibers (Tominaga and Julius, 2000; Julius and Basbaum, 2001; Dhaka et al., 2006; Bandell et al., 2007; Caterina, 2007). In a recent review Saito and Shingai (2006) reported that all the thermosensing related TRP channels except the TRPM4 are present in the chicken genome but that their mechanism and tuning have changed through vertebrate evolution. Differences among animals have been reported regarding the sensitivity of the somatosensing system. A sigmoid type response of the trigeminal nerve to capsaicin has been reported for both mammals and chickens. However, the responsive concentration range to capsaicin in lab rodents is in the nM (Toth et al., 2004) while in chickens is in the μM and does not result in a full neuronal response, such as in rodents (Kirifides et al., 2004). Furthermore, capsaicin-sensitive responses in chickens seem to be TRPV1-independent (Mahmoud et al., 2007) and are not associated with pain-producing effects (Jordt and Julius, 2002). While most ‘mammal’ responses to spices seem to be pain-mediated, birds are more tolerant. Mammalian predators are repelled by the pepper plant whereas birds are favoured as vectors for seed dispersal (Tewksbury et al., 1999; Tewksbury and Nabhan, 2001; Jordt and Julius, 2002; Nolte et al., 1993; Clark, 1998). Mammals, including humans and pigs, show strong aversive responses to oral capsaicin (Green, 1989) and also to cinnamaldehyde, carvacrol or formic acid (Bikker et al., 2003; Eisemann and van Heugten, 2007), but birds are indifferent to exposures of up to 20,000 p.p.m. capsaicin and other EOS mixtures (Szolcsanyi et al., 1986; Mason et al., 1991; Roura et al., 2008).

Birds do not show behavioural responses to capsaicin, nevertheless the avian nervous system is not insensitive to this compound (Sann et al., 1987; Harti et al., 1989). Chickens may respond to low levels of spices in feed by increasing digestive secretions without significantly rejecting feed (i.e., decreasing feed intake), as opposed to mammals responding with a higher degree of feed refusal. For example, a significant increase in pancreatic amylase, trypsin and maltase activities in broilers fed different blends of commercial EOs has been reported (Williams and Losa, 2001; Jang et al., 2004, 2007). However, Lee et al. (2003) showed no clear effects on enzyme activities in chickens fed dietary thymol and cinnamaldehyde after 21 or 40 days. The effect of EOs on nutrient digestibility in chickens has been studied by several groups. The inclusion of a labiatae extract and blends containing carvacrol, cinnamaldehyde and capsaicin increased apparent fecal digestibility of dry matter and the digestibility of ether extract (Hernández et al., 2004), fiber, fat, ash and protein (Jamroz et al., 2003). Additionally, the labiatae counteracted the carboxymethyl cellulose suppressive effect on fat digestibility in chickens (Lee et al., 2004).

The influence of spices on lipid metabolism has captured particular attention since it has become apparent that oral capsaicin may regulate adipose tissue distribution. In rodents capsaicin reduced weight of visceral (perirenal) fat and this may be attributed to an increase in TRPV1 expression (Leung, 2008). The activation of TRPV1 channels by capsaicin prevented adipogenesis in 3T3-L1-preadipocytes and visceral adipose tissue from mice and humans (Zhang et al., 2007). Furthermore, hepatic cholesterol was lowered by dietary curcumin and capsaicin in rats (Manjunatha and Srinivasan, 2007). Very little is known on the potential effects of EOs in lipid metabolism in chickens. A dose-dependent decrease in serum cholesterol was reported in cockerels fed dietary limonene (Qureshi et al., 1988) but no changes in plasma cholesterol were found in layers after dietary supplementation with terpineol, citronellol and geraniol (Hood et al., 1978). The potential relevance of these findings merits further research in poultry.

4.2. Antioxidant: preventing tissue oxidation

Antioxidants have been widely used as food additives to provide protection against oxidative degradation of foods by free radicals. Since ancient times, spices used in different types of food to improve flavours are known to have antioxidant capacities. In order to prolong the storage stability of foods, synthetic antioxidants are used for industrial processing. Nevertheless some of the commonly used synthetic antioxidants such as butylated hydroxytoluene (BHT) and butylated hydroxyanisole (BHA) have come into question due to their suspected carcinogenic potential as evidenced by toxicologists (Reishe et al., 1998). Furthermore, the general consumer rejection to synthetic food additives has been increasing in modern times. For this reason, there is a growing interest in studies of natural additives as potential antioxidants.

Many sources of antioxidants of plant origin have been studied in recent years. Among these, the antioxidant properties of many aromatic plants and spices have shown to be effective in retarding the process of lipid peroxidation in oils and fatty foods and have gained the interest of many research groups.

Herbs of the Labiatae family, particularly rosemary, oregano and sage, have been extensively studied for their antioxidant activity. Oregano, a characteristic spice of the Mediterranean cuisine obtained by drying leaves and flowers of *Origanum vulgare* subsp. *hirtum* plants, is well known for its antioxidant activity and shows a considerable effect on preventing or delaying the process of lard oxidation (Economou et al., 1991). The oregano essential oil was fractionated according to acidity and polarity, in order to correlate properly the antioxidant activity to the chemical composition. Carvacrol and thymol, the two main phenols that constitute about 78–82% of the essential oil of oregano, are principally responsible for this activity (Yanishlieva and Marinova, 1995; Yanishlieva et al., 1999). In addition, other minor constituents such as γ-terpinene and *p*-cymene, two monoterpene hydrocarbons that constitute about 5 and 7% of the total oil, respectively, also contribute to this activity (Adam et al., 1998). Recent publications (Cervato et al., 2000; Abdalla and Roozen, 2001; Damechki et al., 2001; Martinez-Tomé et al., 2001; Vichi et al., 2001; Bendini et al., 2002) also showed antioxidant activities of oregano.

Preliminary studies of the antioxidant activity of cinnamon have also been demonstrated by Kamel (1999). Three cinnamon extracts of different commercial origins showed antioxidant activity comparable to the synthetic antioxidant BHT. The antioxidant activity of some herbs has been detected by the Rancimat test. Scheeder (2000) showed the antioxidant capacity of Rosemary and its extract, olive leaf extract as well as different tea samples.

The antioxidant activity of phenolic compounds in plants is mainly due to their redox properties and chemical structure. Farag et al. (1989a) discussed the relationship between the antioxidant property and the chemical composition of the EOs. It was suggested that the high antioxidant activity of thymol is due to the presence of phenolic OH groups which act as hydrogen donors to the peroxy radicals produced during the first step in lipid oxidation, thus retarding the hydroxy peroxide formation. Teissedre and Waterhouse (2000) reported a high correlation between the total phenol content of EOs and human low-density lipoprotein oxidation *in vitro*.

Lipid oxidation is a major problem encountered during meat processing, cooking, and refrigerated storage. It affects the quality of the product due to loss of desirable colour, odour and flavour, and shortens shelf-life (Maraschiello et al., 1998). Poultry meat has many desirable nutritional characteristic such as low lipid content and relatively high concentrations of polyunsaturated fatty acids that can be further increased by specific dietary strategies. Due to this relatively high content of polyunsaturated fatty acids, poultry meat is particularly susceptible to oxidative deterioration, with oxidation often determining the shelf life of pre-cooked, refrigerated ready-to-eat products (Igene and Pearson, 1979). The susceptibility to oxidative deterioration is higher for turkey meat compared to chicken meat, although these two species have similar tissue fatty acid compositions (Marusich et al., 1975). The difference has been attributed primarily to the weaker ability of turkeys to store dietary tocopherol in their tissues compared to chickens (Sklan et al., 1982; Wen et al., 1997). Within tissues, α-tocopherol is localized in the highly unsaturated phospholipid bilayer of the cell membranes where it inhibits lipid oxidation by functioning as a free-radical scavenger. Hence, the antioxidant capacity of poultry meat depends largely on the concentration α-tocopherol, which in turn is dependent on the level of α-tocopheryl acetate added in the diet (Wen et al., 1997).

Antioxidant properties of EOs based on animal studies have been investigated by Youdim and Deans (1999a,b, 2000). Rats fed thyme oil and thymol maintained higher levels of polyunsaturated fatty acids in the phospholipids fractions of different tissues. These supplements acted as an effective free radical scavengers and also influenced the *in vivo* antioxidant defense systems in the animal. There is also evidence in laying hens, that the reduction of lipid oxidation in refrigerated egg yolk by the addition of thymol in the diet, measured by malondialdehyde formation, may prolong storage time and reduce or eliminate the need for additional oxidative stabilization (Botsoglou et al., 1997). Thymol and cymene-2,3-diol, which are responsible for the antioxidant of thyme, have been measured in eggs collected during 24 day feeding period (Krause and Ternes, 1999). Approximately, 0.004 and 0.006% of the ingested cymene-2,3-diol and thymol were transferred to egg yolk after 12 days of feeding. The compounds disappeared from egg yolk soon after supplementation was ceased.

Apart from tocopherol, additional dietary natural antioxidants such as extracts of rosemary (Lopez-Bote et al., 1998) or tea catechins (Tang et al., 2000) have also been shown to have the potential to increase the antioxidant capacity of chicken meat. In addition, dietary oregano essential oil improves the oxidative stability of raw or precooked chicken meat during refrigerated storage (Botsoglou et al., 2003b, 2004; Young et al., 2003). Dietary supplementation with herbs and herb extracts is a simple and convenient strategy to introduce a natural antioxidant into chicken meat.

Alternative natural antioxidants have also been evaluated as a dietary supplement for turkeys. The effect of dietary oregano essential oil and α-tocopheryl acetate supplementation on the susceptibility of raw and cooked turkey meat to lipid oxidation during refrigerated storage and on iron-induced lipid oxidation has been determined by Botsoglou et al. (2002a,b), Botsoglou et al. (2003a,b,c) and Papageorgiou et al. (2003). The results presented in these studies show an increase in the antioxidant capacity of turkey tissues as a result of dietary oregano oil and/or α-tocopheryl acetate supplementation. Inclusion of 200 mg oregano oil/kg diet was more effective in delaying lipid oxidation compared with the inclusion of 100 mg/kg, but equivalent to the inclusion of 200 mg/kg α-tocopheryl acetate. Likewise, Marcincak et al. (2008) showed that the addition of oregano essential oil in broiler diets was effective in delaying lipid oxidation compared to the control diet. The better oxidative stability of meat samples from turkeys and broilers receiving the diets supplemented with oregano oil was probably the result of antioxidant constituents of the oregano oil that entered the circulatory system and were distributed and retained in meat. Their impact on sensory quality of poultry meat has been regarded as minor (Vogt and Rauch, 1991) and EOs deposited in poultry tissue can be consumed by human. However, a reliable laboratory method to determine EOs in biological system is necessary to identify and quantify of any of these oils at low levels in tissues.

4.3. Antimicrobial activity and modulation of gut microbiota

One of the most evident intrinsic effects of plant extracts is their antimicrobial activity. There is an innumerable list of references in the scientific literature providing clear *in vitro* evidence of the antibacterial, antifungal and antiviral activity of many extracts against animals and/or foodborne pathogens (Larrondo et al., 1995; Nenoff et al., 1996; Basílico and Basílico, 1999; Tabak et al., 1999; Dorman and Deans, 2000; Rota et al., 2004). For example, Cowan et al. (1999) reported that 60% of essential oil derivatives examined to date were inhibitory to fungi while 30% inhibited bacteria.

Most studies investigating the action of whole EOs against food spoilage organisms and foodborne pathogens agree that, generally, EOs are slightly more active against Gram-positive than Gram-negative bacteria (Table 3). Chao et al. (2000) investigated the effects of 45 essential oils on a broad spectrum of micro-organisms, which included eight different genera of bacteria, four of which were Gram-positive and four of which were Gram-negative. They concluded that Gram-negative bacteria were more resistant to the essential oil tested than the Gram-positive bacteria. Oils from cinnamon bark, savory and rosewood were effective against both the Gram-positive and Gram negative bacteria. Similar inhibitory results have been obtained by Smith-Palmer et al. (1998) on five food-borne pathogens (*E. coli*, *S. enteritidis*, *C. jejuni*, *S. aureus*, *L. monocytogenes*) with cinnamon, clove and thyme essential oils. However, coriander EO only inhibited the Gram-positive bacteria (Chao et al., 2000). It is known that the chemical composition of EOs from a particular plant species can vary according to the geographical origin and harvesting period. It is therefore possible that variation in composition between batches of EOs is sufficient to cause variability in the degree of susceptibility of Gram-negative and Gram-positive bacteria.

The minimum inhibitory concentration (MIC) is a measure of EOs antibacterial capacity. A selection of MICs for EOs and EO components tested in vitro against food borne pathogens are presented in Table 3. Some studies have concluded that whole EOs have greater antibacterial activity than their major components (Gill et al., 2002; Mourey and Canillac, 2002), which suggests that the minor components are critical to the activity and may have a synergistic effect or potential influence. The two structurally similar major components of oregano EO, carvacrol and thymol, were found to give an additive effect when tested against *S. aureus* and *P. aeruginosa* (Lambert et al., 2001). Synergism between carvacrol and its biological precursor *p*-cymene has been noted when acting on *B. cereus* vegetative cells. It appears that *p*-cymene, a very weak antibacterial, swells bacterial cell membranes to a greater extent than carvacrol does. By this mechanism *p*-cymene probably enables carvacrol to be more easily transported into the cell so that a synergistic effect is achieved when the two are used together (Ultee et al., 2002).

Although the antimicrobial properties of EOs and their components have been reviewed extensively in the past, the mechanism of action has not been studied in great detail (Lambert et al., 2001). Considering the large number of different groups of chemical compounds present in EOs, it is most likely that their antibacterial activity is not attributable to one specific mechanism but that there are several targets in the cell (Skandamis et al., 2001; Carson et al., 2002). An important characteristic of EOs and their components is their hydrophobicity, which enables them to partition lipids in the bacterial

Table 3
Effect of essential oils on the growth inhibition of bacteria (adapted from Chao et al., 2000).

Essential oil	Zone of inhibition							
	Gram-positive bacteria				Gram-negative bacteria			
	Bc	Ml	Sa	Ef	Ec	Af	Ecl	Pa
Angelica	2	4	4	4	2	7	1	–
Bergamot	4	6	2	4	2	3	1	–
Cinnamon	17	27	9	12	12	24	18	6
Coriander	>33	>33	25	33	–	10	–	–
Dill	4	4	5	3	4	7	1	1
Eucalyptus	>33	4	–	–	1	7	2	–
Ginger	2	2	–	1	–	–	–	–
Juniperberry	4	7	3	2	2	10	1	–
Lime	4	2	2	2	–	7	–	1
Mandarine	3	–	4	4	1	6	–	–
Savory	15	>33	10	15	18	30	17	–
Nutmeg	2	2	2	1	5	5	3	–
Orange	–	3	–	2	1	5	–	–
Pepper	1	2	–	–	–	8	–	–
Pine	5	5	3	4	3	14	–	–
Rosemary	3	2	–	–	6	6	3	–
Rosewood	13	17	7	5	12	19	15	–
Sage	2	4	2	1	2	12	2	–
Tarragon	4	6	6	7	3	12	1	–

Bc, Bacillus cereus; Ml, Microccocus luteus; Sa, Staphylococcus aureus; Ef, Streptococcus faecalis; Ec, enterobacter cloacae;Af, Alcaligenes faecalis; Ecl, Escherichia coli; Pa, Pseudomonas aeruginosa.

cell wall and mitochondria, disturbing the structures and rendering them more permeable. Generally, the EOs possessing the strongest antibacterial properties against food borne pathogens contain a high percentage of phenolic compounds such as carvacrol, eugenol (2-methoxy-4-(2-propenyl)phenol) and thymol (Farag et al., 1989a, 1989b; Thoroski et al., 1989; Cosentino et al., 1999; Dorman and Deans, 2000; Juliano et al., 2000; Lambert et al., 2001). Carvacrol and thymol are able to disintegrate the outer membrane of Gram-negative bacteria, releasing lipopolysaccharides and increasing the permeability of the cytoplasmic membrane to ATP and depolarize the cytoplasmic membrane (Helander et al., 1998; Xu et al., 2008).

Fractions of cilantro, coriander, dill and eucalyptus EOs (each containing several components), when mixed in various combinations, resulted in additive, synergistic or antagonistic effects (Delaquis et al., 2002). A mixture of cinnamaldehyde and eugenol at 250 and 500 $\mu g\,ml^{-1}$, respectively, inhibited growth of *Staphylococcus* sp., *Micrococcus* sp. *Bacillus* sp. and *Enterobacter* sp. for more than 30 days completely, whereas the substrates applied individually did not inhibit growth (Moleyar and Narasimham, 1992).

For many years, herbs and spices and their EOs have been used as pharmaceuticals in alternative medicine and as a natural therapy. The antibacterial effect of EOs is well established (Dorman and Deans, 2000), and it has been described in the first part of this section. However, all these tests were performed *in vitro* with only a limited number of trials performed in animals. For that reason, studies aimed to evaluate the use of natural plant bioactive chemicals and blends as supplements to combat disease or modify the GI microbiota composition and population in growing birds are relevant.

The effect of two different blends of EO components on the proliferation of *C. perfringens* in the intestines and excreta of broiler chickens was tested by Mitsch et al. (2004). The results indicate that blending thymol, eugenol, curcumin and piperin or carvacrol and thymol (50% each), eugenol, curcumin and piperin can reduce *C. perfringens* colonization and proliferation in the broiler gut. The authors inferred that the effects of the product are due partly to a direct inhibition of the bacteria. However, digestive enzymes induced by EOs could also increase nutrient digestibility and improve the regulation and stabilization of the gut microbiota. Inactivation of *C. perfringens* toxins by digestive enzymes, such as trypsin (Arbuckle, 1972; Baba et al., 1992), could also explain why colonization of this bacteria was reduced in the chicken gut by the EOs. Similar results have been presented by Sims et al. (2004) who demonstrated that *C. perfringens*-challenged broilers receiving a commercial blend or bacitracin had less intestinal lesions and performed better than or similar to equally challenged control birds. Cross et al. (2002) and Jang et al. (2007) have also reported a reduction on coliform counts in birds supplemented with thyme oil or commercial blend of EOs including thymol. Similarly, a blend of capsicum, cinnamaldehyde and carvacrol lowered the number of *E. coli* and *C. perfringens* (Losa and Köler, 2001; Tucker, 2002; Jamroz et al., 2003). Tellez et al. (1993) and Orndorff et al. (2005) in chickens and Vicente et al. (2007) in laying hens also showed the prophylactic effect of capsaicin on experimental *S. enteritidis*. However, Cross et al. (2007) showed no effect on the intestinal microbiota populations after the inclusion of culinary herbs or their EOs. Plant extracts in diets may therefore affect gut microbiota, although the chemical composition of the extract appears to be important in obtaining the optimal effects and it is speculated that the *in vivo* antimicrobial property of EOs in birds can be influenced by basal diet and environmental conditions.

Studies have also been published on the effect of EOs on the control of coccidiosis in poultry. The effect of different treatments on the performance of broiler chickens infected with *Eimeria acervulina* was investigated. Ibrir et al. (2002) with thyme, Giannenas et al. (2003) with oregano and Christaki et al. (2004) with a commercial preparation, found no effect of the treatments on oocysts excretion, but showed a significant beneficial effect on post-infection performance and also a significant reduction in the presence of blood in faeces. Evans et al. (2001) reported a reduced oocyte excretion in chicks fed diets containing 50 ppm of a mixture of EOs (clove, 1%; thyme, 0.1%; peppermint, 0.1% and lemon, 0.1%) compared to those fed an unsupplemented diet. Waldenstedt (2003) showed that vaccination against coccidiosis in combination with an oregano based commercial product may be an alternative control method for intestinal health in organically produced chickens. Recently, Oviedo-Rondón et al. (2006) and Hume et al. (2006) have demonstrated that a commercial blend of EOs modulate microbial communities in cocci-vaccinated broilers, avoiding drastic shifts after mixed coccidian infection.

Studies on the morphological and histological responses of the chicken intestinal tract to the addition of EOs have also been conducted. Jamroz et al. (2006) reported the increase in mucus release and the thickness of the mucus layer on glandular stomach and wall of jejunum in chicken fed diets with plant extracts. These findings suggest villi-related protective properties of dietary carvacrol, cinamaldehyde and capsaicin mixtures in chickens. Furthermore, the changes in the mucus layer will in turn reduce the chances of epithelial microbial adhesion therefore hypothetically changing the gut microbial population.

5. Metabolic pathway and toxicity of bioactive components of EOS

The metabolic pathways of various pure components of EOs that are used in herbal medicine have been recorded by Kohlert et al. (2000). The bioactive substances are quickly absorbed after oral, pulmonary, or dermal administration and most are metabolised and either eliminated by the kidneys in the form of glucuronides or exhaled as CO_2. For that reason, their accumulation in the body is unlikely due to rapid clearance and short half lives.

The degradation and kinetics of carvacrol, thymol, eugenol and trans-cinnamaldehyde in the GI tract of piglets have been recently reported by Michiels et al. (2008). These authors developed a method to determine the composition of these EOs and demonstrated that they were mainly and almost completely absorbed in the stomach and the proximal small intestine. Besides the metabolism by the host, it seems unlikely that the intestinal microbiota could metabolise the EOs. Varel and Miller (2000) and Varel (2002) reported that thymol and carvacrol were not metabolised by microorganisms residing in swine feces. Studies on oral toxicity in rat reported by Jenner et al. (1964) showed that the acute oral LD50 (mg/kg of body weight) with carvacrol, cinnamaldehyde, beta-ionone and thymol was 810, 2220, 4590 and 980, respectively. However, when rats were fed diets containing thymol at the level of 1000 and 10,000 ppm, no clear signs of toxicity were observed (Hagan et al., 1967). Urinary metabolites of cinnamaldehyde have also been studied in rats and mice (Peters and Caldwel, 1994). Cinnamaldehyde was rapidly excreted via urine in the first 24 h and less than 2% of the administered doses remained in the carcass. A low bioavailability of less than 20% was shown in gavaged rats fed with doses of 250 and 500 mg/kg of cinanmaldehyde (Yuan et al., 1993).

Igimi et al. (1974) and Kodama et al. (1974) studied the metabolic effect of d-limonene in rats and rabbits. They reported that d-limonene absorbed from the intestine was rapidly excreted without significant deposition in the body. Similar results have been obtained by Austgulen et al. (1987) and Takada et al. (1979) in rats and rabbits fed carvacrol and thymol. Large quantities of these compounds were excreted in unchanged form.

6. Conclusions and areas for future research

The increasing pressure on the livestock industry to reduce or eliminate feed-antibiotics as growth enhancers has initiated new research to find safe and efficient alternatives. This new generation of feed additives includes herbs and EOs. The beneficial effects of most herbs, spices and their bioactive compounds have been recognised since antiquity and their properties reported in foods and experimental animals.

A wide range of plants contain bioactive compounds which have the potential to act as multifunctional feed supplements for animals. Some extracts from common herbs and spices are reported to have multiple actions in monogastric animals including effects on performance, the oronasal somatosensing and the digestive systems, lipid metabolism, prevention of tissue oxidation and modulating microbial populations. Therefore the effect of EOs may not only be confined to the microbiota, but may extend to peripheral chemosensing and animal metabolism. A better knowledge of the mechanism of action and effects of individual compounds would be useful to formulate mixtures of compounds to optimize efficacy.

In order to utilise and exploit this potential research should focus on:

- More information should be pursued with respect to the specific class of EOs in studies in vivo on their dose-responses, their effect in combination with different commercial feed formulations and the contribution of animal genetics and rearing conditions to better explain their practical applications for the animal sciences.
- In expectation of a wide use of these extracts in the food and the feed industries as natural additives, analytical methods for the traceability of the active compounds in food and feed products are required. There has not been yet developed an analytical method suitable for identification and quantification of traces of essential oil constituents in feeds and animal tissues. These analytical techniques will be vital for implementing programmes of feed traceability and residue levels in carcasses, eggs and milk. The stability of some EO compounds during feed processing should particularly be adressed.
- Identification and standardisation of the active substances. The inclusion of a single herb or its extracted essential oil in diets may not always have a similar effect on broiler performance, therefore it is necessary to measure the chemical quality in a plant extract to identify optimal compositions of secondary plant compounds for future reference.

- Interactions between EOs and their components and other feed ingredients and feed additives need to be investigated. This complexity in terms of the number and the variability of bioactive compounds, and the interactions between them, is a major limitation to the rate of progress that is being made in this area of research, where raw plant materials and plant extract preparations are being studied. Synergistic effects could be exploited so as to maximise the antibacterial activity of EOs and to minimise the concentrations required to achieve a particular antibacterial effect. Potential interactions with other feed additives such as organic acids and probiotics among others should also be addressed.

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