Understanding the nutritional chemistry of lupin (Lupinus spp.) seed to improve livestock production efficiency

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Abstract
In their raw, unprocessed form, lupins have many desirable characteristics for feeding both ruminants and single-stomached animals. An emphasis on these desirable characteristics when formulating diets, combined with an advanced knowledge of how components of lupins can influence nutritional value, will ensure they make a cost-effective contribution to livestock diets. The main lupin species used in livestock diets include Lupinus albus, L. angustifolius and L. luteus. Supplementation of ruminant diets with lupins has been shown to have many positive effects in terms of growth and reproductive efficiency, comparable with supplements of cereal grain. The true value of lupins in ruminants, however, can only be determined following a better definition of animal requirements and a closer match of ration specifications. Pigs can effectively utilize L. angustifolius and L. luteus, but detailed research has yet to reveal the reason for poor utilization of diets containing L. albus. Poultry can tolerate high levels of lupins in their diets but levels are often restricted to avoid problems associated with excess moisture in the excreta. Variable responses to enzymes have been observed when attempting to rectify this problem. Lupins have unique carbohydrate properties characterized by negligible levels of starch, high levels of soluble and insoluble NSP, and high levels of raffinose oligosaccharides, all of which can affect the utilization of energy and the digestion of other nutrients in the diet. In addition to carbohydrates, an understanding of lupin protein, lipid and mineral composition together with a knowledge of potential anti-nutritional compounds is required if the use of this legume is to be optimized.

Lupins: Growth performance: Feed composition

Introduction
Considerable effort has been invested into research to define the nutritional value of lupins for livestock. Based on their chemical composition alone, it is obvious that lupins have significant potential as a protein and energy source for livestock. The composition of lupins is, however, characterized by negligible levels of starch, high levels of soluble and insoluble NSP, low levels of sulfur amino acids and variable levels of lipid (Petterson et al. 1997). Consequently, the nutritional chemistry of lupins has presented many challenges to nutritionists and it is only through an understanding of the physiological responses of livestock to the presence of lupins

Abbreviations: DE, digestible energy; ME, metabolizable energy; VFI, voluntary feed intake.
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in diets that production efficiency can be improved. The unique structure of lupins has also made them a model for the assessment of the role of components such as NSP in livestock diets, thus increasing the proportion of research conducted with lupins relative to the quantities available for livestock production worldwide.

In a world with advanced genetic engineering and plant breeding capabilities, animal nutritionists are frequently asked to identify those characteristics of grain crops that could be altered to improve their nutritional value for livestock. Lupins in particular, with their unique physical and chemical characteristics, are a frequent target. In response to such requests, van Barneveld & Hughes (1994) made concise recommendations to lupin breeders in relation to potential changes to the physical and chemical properties of lupins and lupin agronomy that could greatly enhance the nutritive value of lupins for single-stomached animals. A response of this nature could be considered irresponsible as modifications to lupins to improve their nutritive value for single-stomached animals will undoubtedly decrease their nutritive value for other classes of livestock, such as ruminants. For example, increases in the starch content and a reduction in the level of soluble and insoluble NSP in lupins will increase the energy yield for single-stomached animals and may improve the digestibility and availability of amino acids, but these changes will substantially increase the risk of acidosis when lupins are fed to ruminants.

As nutritionists, we are not seeking a nutritionally ideal single feed ingredient. It is the role of the nutritionist to develop nutritionally complete livestock diets from a combination of complementary feed ingredients based on an understanding of nutritional value. The fact that lupins present more challenges than a feed ingredient such as soyabean meal should not pre-dispose them to wholesale genetic manipulation. In their raw unprocessed form, lupins have many desirable characteristics for feeding both single-stomached animals and ruminants. An emphasis on these desirable characteristics when formulating diets and an advanced knowledge of how components of lupins can influence nutritional value will ensure they make a cost-effective contribution to livestock diets.

The objectives of this review are to (1) identify those lupin species used in livestock production, (2) examine livestock production responses to lupins to demonstrate the need to understand the nutritional chemistry of this legume, and (3) discuss the characteristics of lupin carbohydrates, proteins and amino acids, lipids, minerals and anti-nutritional compounds.

A significant proportion of the discussion in this review is based on Australian data or circumstances, as the dominant producer of lupins worldwide. Relevant international data has been cited where appropriate; however, it should be noted that a large amount of international livestock nutrition research with lupins is based on samples originally sourced from Australia. This review also serves to deliver outcomes from recent collaborative research completed in Australia and France having been initiated and funded by the Grain Pool of Western Australia, the Grains Research and Development Corporation and the Pig Research and Development Corporation.

Lupin species used in livestock production

Lupins are increasing in importance as a component of livestock diets worldwide, with more than half the total lupin production in the world occurring in Australia (Landers, 1991). Coffey (1994) estimated that 2 million tonnes of lupins will be produced in Australia by the year 2000, of which 500,000 tonnes will be used for domestic consumption with the remainder exported. The vast bulk of lupins produced are used as livestock feed with significant potential for an
increase in consumption. For example, Edwards (1994) estimated that there is a potential market exceeding 1.13 million tonnes for lupins as a feed ingredient for all intensive classes of livestock (pigs, poultry, dairy cattle, feedlot beef) in Australia alone. In addition, Murray (1994) estimated that sheep in Western Australia consume up to 550,000 tonnes of lupin grain, not to mention the significant quantity of lupin residues grazed by sheep, each year.

Lupin species and cultivars used in livestock production are governed by the growing region and/or the livestock systems’ proximity to markets as well as their nutritional value for different livestock classes. Five lupin species, *Lupinus angustifolius*, *L. albus*, *L. atlanticus*, *L. consentinii* and *L. luteus* have been fully domesticated from old world species originating from around the Mediterranean basin and North Africa, with another, *L. pilosus*, approaching this status. Despite the existence of 150–500 species of New World (Americas) lupins, most are perennial, rangeland species with small seeds, and hence have not been widely domesticated (DS Petterson, personal communication).

By far the greatest form of lupin utilization in Australia is as a whole-grain supplement to grazing sheep fed on low-grade roughage. This whole-grain supplement can be offered as part of a grazing crop, where sheep, but not cattle, have been shown to be effective harvesters of the seed (Carbon *et al.* 1972), or fed back to the animal following harvest of the seed. Responses vary depending on the quality of the roughage on offer. *L. angustifolius* is widely used as a supplementary feed for ruminants in Australia during the summer–autumn period, especially for weaners, pregnant ewes and dry sheep, due to a lack of high quality feed. There are few comparisons of the performance of ruminants on different species or cultivars of lupin grain; however, supplementation of ruminant diets with grain from *L. albus*, *L. angustifolius*, *L. luteus* and *L. consentinii* have all been shown to improve intake and subsequent animal performance depending on the quality of the roughage being fed simultaneously (Kennedy & Smith, 1985; Morcombe *et al.* 1986; Godfrey *et al.* 1993; Murray, 1994).

In Australia, there are three main species of lupins used in pig diets: *L. angustifolius*, *L. albus* and *L. luteus*. *L. angustifolius* is a valuable feed ingredient for the pig industry and can be used effectively in diets for most classes of pigs. *L. albus* is currently not recommended for use in pig diets due to resulting depressions in pig growth rates, with commercial nutritionists formulating diets for large Australian piggeries demonstrating poor returns when *L. albus* is used (Edwards & van Barneveld, 1998). The main reason for reduced growth rates when *L. albus* is included in pig diets at levels above 150 g/kg (Standing Committee on Agriculture, 1987) is reduced feed intake. There has been some success identifying the factors responsible for this reduction in feed intake associated with feeding *L. albus*, yet to date we have no means of manipulating these factors so that the pig industry can exploit the comparatively higher protein, lipid and reduced NSP content of this lupin. *L. luteus* (yellow lupin) has only recently been assessed as a feed ingredient for pigs (Mullan *et al.* 1997) and has significant potential. This lupin is native to Portugal, Western Spain and the wetter parts of Morocco and Algeria. Recent selections of *L. luteus* have been found to have a higher crude protein content (380 g/kg, air-DM basis) than either *L. angustifolius* (320 g/kg, air-DM basis) or *L. albus* (360 g/kg, air-DM basis; Petterson *et al.* 1997) and to yield better than *L. angustifolius* on acid soils of low fertility (700 v. 400 kg/ha, respectively; Mullan *et al.* 1997).

Poultry have a high capacity to utilize the amino acids and energy contained within lupins. While high NSP levels depress the total apparent metabolizable energy (ME) available to poultry, the presence of the lupin NSP has a minimal impact on the ability of poultry to utilize other nutrients in the diet, compared with pigs. Grains of *L. angustifolius*, *L. albus* and *L. luteus* are now an established component in poultry diets, yet despite their high value as a feed ingredient, they are not widely used in many countries.
Livestock production responses to lupins

Ruminants

Supplementation of ruminant diets with lupins has been shown to have many positive effects in terms of growth and reproductive efficiency, comparable with supplements of cereal grain. This is primarily due to the protein contribution from lupins as a N source for microbial protein synthesis, but also possibly due to a higher ME content and less disturbance to fibre digestion which often accompanies the fermentation of cereal starch (Dixon & Hosking, 1992). Consistent with this, Hynd et al. (1985) hypothesized that the predominance of β-galactan in lupins compared with starch in most cereals may affect the rumen microbial population. It was demonstrated that the concentration of protozoa in the rumen fluid of cows fed on hay plus barley was 2–4 times higher than for cows fed on hay plus lupin grain or hay alone. As high concentrations of protozoa in the rumen reduce protein yield to the host, it was concluded that some of the differences in the nutritive value of barley and lupin grains in protein limited systems may relate to their differential effects on protozoa numbers.

Fukamchi (1986) demonstrated that rations containing 100 g flaked lupin/kg diet for milking cows as a replacement for soyabean meal produced similar milk yields and milk quality and did not affect feed intake when the rations were formulated to contain equal levels of DM, crude protein and digestible crude protein. This study is one of the few conducted with ruminants that attempts to equalize the nutritional inputs when assessing this legume. In many studies with ruminants, the positive responses recorded when lupins are fed are a result of an increased nutrient supply to the animal rather than specific beneficial components within the lupins. Often the control within the experiment consists of moderate quality pasture with no grain or grain–legume supplementation (Carbon et al. 1972; Arnold & Charlick, 1976; Arnold et al. 1976; Searle & Graham, 1980; Hawthorne, 1982, 1984; Hodge et al. 1982; Hawthorn & Stacey, 1984; Barker et al. 1985; Butler & McDonald, 1986; Morcombe et al. 1987; Rojas & Carrasco, 1987; Cottle, 1988; Curtis & Mavrantonis, 1990; Hinch & Thwaites, 1990; Morcombe & Ferguson, 1990; Robertson & Hinch, 1990; Thompson & Curtis, 1990; Godfrey et al. 1993; May et al. 1993). Similarly, comparisons between lupins and other grain legumes as a nutrient source for ruminants often reflects differences in the total content of nutrients, rather than superior digestibility or feeding qualities (e.g. Arnold & Wallace, 1977; Arnold et al. 1977; Guillaume et al. 1987).

Lupins do possess some inherent characteristics that make them a more desirable supplement in ruminant rations. For example, ME derived from lupin seeds (particularly via fermentation to acetate) makes them a valuable supplement for the improvement of reproductive performance in sheep. Increases in the ovulation rate of sheep fed lupin seed supplements have been consistently demonstrated (Lindsay, 1976; Johnsson et al. 1982; Leury et al. 1990). Lindsay (1976) and Nottle et al. (1985) suggested that a unique feature of the response of sheep to lupin seed is that ovulation rate increases without a measurable change in liveweight, possibly due to the high protein content of the grain. Subsequent studies by Fletcher (1981) and Rowe et al. (1983) demonstrated that increased protein intake per se stimulates the ovulation rate only when the initial intake is close to the maintenance requirement, and that ME, either by itself or together with protein, subsequently becomes the limiting factor. Teleni et al. (1989a) conducted experiments to provide insights into the mechanisms by which supplements of lupin grain stimulate ovulation rate. In particular, quantitative data were collected on the metabolism of acetate and glucose in ewes fed on lupin grain in amounts found to stimulate ovulation rate. It was concluded that ewes fed on a maintenance basal diet and a supplement of 750 g lupin
grain/d would rapidly switch to the anabolic mode concomitant with increases in glucose entry rate by more than 100% and acetate entry rate by more than 50%. This supports the hypothesis suggested by Teleni et al. (1989b) that the principal nutritional factors that stimulate increases in ovulation rate in ewes fed on a supplement of lupin grain are the energy yielding nutrients when fed at levels above maintenance.

Other inherent characteristics of lupins that support their use in ruminant diets involve their digestibility characteristics. Lupins fed to preruminant calves in diets containing 210 g crude protein/kg and 210 g fat/kg (DM basis) were partially proteolysed and had low antigenic and antitryptic activity (Tukar et al. 1995). As a result, digestibility of N from the lupins was high at the end of the small intestine. Similarly, Valentine & Bartsch (1987) demonstrated that feeding high levels of legume grains, especially lupins, rather than barley grain to dairy cows results in rumen pH values and NH₃-N concentrations that are unlikely to cause significant depressions in the rate of fibre digestion or intake of cereal hay.

The relative value of lupins in ruminant diets will become more apparent as the ability to match nutrient inputs with animal requirements improves. One mechanism to achieve this will be through the use of rumen-flow models coupled with post-ruminal digestion and subsequent utilization models. This is supported by the fact that, in many instances, a combination of lupins and cereal grain may deliver superior performance in ruminants by achieving a closer to optimal balance of nutrients in the total diet (Hodge et al. 1981). Kenney (1980), in a study with lambing ewes under drought feeding conditions, determined the optimum proportion of lupin grain in a lupin–cereal grain supplement to be 300 g/kg. In dairy production, where nutrition of the animals is closely scrutinized compared with sheep or extensive cattle production systems, lupins are seldom fed as the only supplement but more generally in mixtures with cereal grains and other feedstuffs. The level of lupins included in the diet is determined by the protein content of the pasture or conserved fodder on offer, the stage of lactation and level of production, and the cost competitiveness of lupins relative to other protein meals and cereal grains.

The value of lupin grain in dairy diets is not normally assessed on any singular aspect but more on the aggregate of its inherent properties. For example, high energy, high protein, orderly fermentation rate and low acidosis risk (Edwards & van Barneveld, 1998). One positive attribute is its apparent ability to maintain milk fat levels at high levels of supplementation, in contrast to the problems often encountered with similar levels of cereal grain supplementation (Bartsch et al. 1986; Sinclair & Gooden, 1989; Valentine & Bartsch, 1990; Hough & Jacobs, 1994). The explanation for this may involve the orderly rate of fermentation of lupins and the relatively high lipid content of lupins rather than a manipulation of the acetate : propionate ratio in the rumen (Dixon & Hosking, 1992).

A factor confounding our ability to assess the nutritive value of lupins for ruminants is the interaction between supplementary grain and the predominant forage on offer. In situations where lactating dairy cows have a basal diet of low to medium quality pasture or roughage, lupin grain generally produces a better response than barley grain and non-protein N mixtures (Bartsch et al. 1986; Valentine & Bartsch, 1990). Yet where cows are fed on high quality pasture, lactational responses to lupin grain have been similar to those for oat or barley grain (Moate et al. 1984; Valentine & Bartsch, 1989). Further to this, where pastures are high in fermentable N, the addition of lupins to the diet may result in excessive rumen NH₃ levels, leading to high blood urea N levels which are known to have a negative effect on fertility. Consequently, the economic use of lupin grain in dairy diets will require a judgement as to how well the nutrient profile of lupin grain balances the nutritional contribution of the basal feedstuffs, relative to the cost of meeting these from alternative sources (Edwards & van Barneveld, 1998).
One clear message from research involving the feeding of lupin seed to ruminants is that there are few factors within lupins likely to negatively affect ruminant production and the low levels of starch in the seed means there are limited precautions associated with lupin seed supplementation. For this reason, the detailed assessment of the nutritional chemistry of lupins to improve production efficiency in livestock contained within this review will pertain mainly to single-stomached animals.

**Pigs**

An understanding of the nutritional chemistry of lupin seed is important if pig production is to be optimized. The species of lupin can affect production responses, and the presence of lupins in pig diets can affect the utilization of other dietary nutrients and subsequent pig performance.

*L. angustifolius* can be included in pig diets at high levels without affecting feed intake and subsequent performance. Barnett & Batterham (1981) replaced soyabean meal in wheat based diets with *L. angustifolius*, while maintaining lysine and energy levels for pigs weighing 6–20 kg and found that they could tolerate dietary inclusion levels of 430 g/kg diet without depressing growth. Similar results were reported by Pearson & Carr (1976; inclusion up to 370 g/kg diet), Taverner (1975), and Batterham (1979). Edwards & van Barneveld (1998) reported the maximum recommended inclusion levels of *L. angustifolius* in pig diets based on existing data (King, 1990; Standing Committee on Agriculture, 1997) and commercial experience to be 100–150 g/kg diet for weaners (up to 20 kg liveweight), 200–250 g/kg diet for growers (20–50 kg liveweight), 300–350 g/kg diet for finishers (50–100 kg liveweight), 200 g/kg diet in dry-sow diets and 200 g/kg diet in lactating-sow diets.

Production responses to the inclusion of *L. angustifolius* in pig diets can be impaired if the overall NSP content of the diet is high. van Barneveld (1997a,b) determined the apparent ileal amino acid digestibility and digestible energy (DE) of wheat, barley, triticale and *L. angustifolius* (cv Gungurru) and then formulated diets to contain 500 g/kg of each cereal, respectively, and 350 g/kg lupins. Diets were equalized for ileal digestible amino acids with lysine limiting at 0.40 g/MJ DE and the growth rates of pigs fed on these diets determined (Table 1). A highly significant difference was observed in the empty-body-weight gain of pigs fed on the diet containing lupins plus barley compared with lupins plus wheat and lupins plus triticale, respectively. Based on the original diet formulations, all pigs should have grown at the same rate if the apparent ileal lysine digestibility and DE values were additive when the lupins and cereals were combined in a mixed diet. It appears that the anti-nutritive effects of soluble and

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**Table 1.** Daily live weight gain (DRG), daily empty-body-weight-gain (DEBWG) and empty-body-weight feed conversion ratio (EBWFCR) of growing pigs (25–55 kg) fed on diets formulated to provide equal levels of ileal digestible lysine and containing specific combinations of lupins (*L. angustifolius* cv Gungurru) and either wheat, barley or triticale (van Barneveld et al. 1997a).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>DRG (g/d)</th>
<th>DEBWG (g/d)</th>
<th>EBWFCR</th>
</tr>
</thead>
<tbody>
<tr>
<td>+ wheat</td>
<td>677</td>
<td>620&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2.71&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>− barley</td>
<td>662</td>
<td>590&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2.90&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>+ triticale</td>
<td>681</td>
<td>630&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2.60&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>a,b</sup> Values in a column with unlike superscript letters were significantly different (*P*<0.05).
insoluble NSP from lupins and barley are amplified when these feed ingredients are combined. This is an excellent example of how an understanding of the nutritional chemistry of lupins can improve the efficiency of their use.

Kelly et al. (1990) reported that inclusion of L. albus cv Ultra in pig diets at levels above 100 g/kg diet significantly reduced the growth rate of pigs weighing 30–57 kg, while finishing pigs could tolerate dietary inclusion levels of up to 200 g/kg diet. This experiment was conducted with isoenergetic and isonitrogenous diets, with the reduction in growth performance consistent with a reduction in feed intake at higher L. albus inclusion levels. Similar results with L. albus cv Ultra were reported by Donovan et al. (1993) for growing pigs fed on diets with inclusion levels of up to 190 g/kg diet replacing soyabean meal, yet there was no reduction in feed intake by finisher pigs fed on diets with lupin inclusion at this level.

The reduction in feed intake observed with diets containing L. albus cv Ultra has been observed with other cultivars. Zettl et al. (1995) reported a reduction in feed intake when growing and finishing pigs were fed on diets containing more than 100 g L. albus cv Amiga/kg diet, while Kemm et al. (1987) reported that L. albus cv Buttercup with an alkaloid content of greater than 0.5 g/kg significantly depressed feed intake in weaner pigs by up to 21% when included in diets at levels of 120 g/kg. L. albus cv Buttercup with alkaloid levels of 0.1 g/kg had no effect on feed intake when included in the diets at the same level.

Mullan et al. (1997) demonstrated a significant quadratic decline in voluntary feed intake (VFI) as the proportion of L. luteus in pig diets is increased. Despite this, it was concluded that L. luteus has the potential to be a high quality feedstuff for growing pigs with a maximum inclusion level of 180 g/kg diet suggested for animals between 20 and 55 kg liveweight. In contrast, Jacyno et al. (1992b) reported that growing pigs fed on diets containing L. luteus cv Ventus at levels of 120 g/kg diet had a significantly lower daily body weight gain than pigs fed on diets containing either soyabean meal or peas formulated to the same level of DE and available lysine.

**Poultry**

Most commercial broiler chicken growers and stockfeed manufacturers currently use less than 100 g lupins/kg in poultry diets in Australia, yet there is clear evidence from a nutritional perspective that broiler and layer diets can contain much higher levels lupins without any negative influences on production. The basis for the upper inclusion level of 100 g lupins/kg diet lies with the effect of lupin inclusion on excreta moisture content and subsequent litter and environmental conditions for broilers. An understanding of the nutritional chemistry of lupins will facilitate the development of strategies to overcome problems with excreta moisture and could provide the basis for higher levels of lupin inclusion in broiler diets.

Up to 250 g/kg diet of either L. angustifolius or L. albus can be included in broiler diets, without detrimental effects on growth or other production measurements when compared with commercial diets containing other protein sources such as soyabean meal (Bekric et al. 1990; Castanon & Perez Lanzac, 1990; Centeno et al. 1990; Brenes et al. 1993; Roth Maier & Kirchgessner, 1994a). Other studies have indicated even greater inclusions of up to 300–400 g lupin grain/kg can be used without detrimental effects on production provided diets are supplemented with amino acids such as methionine (Perez-Escamilla et al. 1988; Buraczewska et al. 1993). These levels, however, will increase excreta moisture, and should be avoided if broiler health is to be optimized (Hughes et al. 1998).
Despite the findings of Hughes et al. (1998) and others, several detailed European studies on the effects of lupins on faecal DM in chickens record no effects with levels of lupin inclusion in diets even above 200 g/kg diet. For example, Karunajeewa & Bartlett (1985) found that replacing varying proportions, up to 100% of the soyabean meal in broiler diets with grain of *L. albus* tended to cause an increased water intake but did not alter faecal DM content. Similar results were obtained for faecal DM and performance by Schams-Schargh et al. (1994), who used up to 180 g *L. albus*/kg diet. Roth Maier & Kirchgessner (1994a) likewise found no effect of 200 g *L. albus*/kg diet. However, with 250 g/kg or more, feed intake, efficiency of gain and faecal DM declined and the faeces became sticky-wet. Health problems subsequently ensued and it was concluded that no more than 200 g/kg grain should be used in broiler diets. In a further study, involving the inclusion of Roxazyme RG™ enzymes in diets containing up to 450 g lupins/kg diet, production was improved and faecal consistency remained unchanged (Roth Maier & Kirchgessner, 1994b).

Early studies on the inclusion of partly debittered lupins in the diets of laying hens indicated that diets should contain less than 100 g lupins/kg diet if optimum production was to be maintained. Subsequent studies conducted with debittered or low alkaloid varieties of *L. albus*, *L. luteus*, *L. mutabilis* and *L. angustifolius* indicated that optimum production could be maintained with between 100 and 200 g lupin grain/kg diet, provided supplements of amino acids are included (e.g. Castanon & Perez Lanzac, 1990; Vogt, 1991; Roth Maier & Kirchgessner, 1995). Despite the smaller influence of increases in excreta moisture on the health of caged laying hens, compared with broilers (due to separation of the hens from their litter) and recognition that layer diets can contain higher levels of lupins than broiler diets, levels of lupins in layer diets should be monitored to ensure excreta odour is minimized and shed conditions optimized in order to maintain egg cleanliness.

**Fish**

Due to a comparatively limited knowledge of the nutritional requirements of fish, it is highly likely that diets are formulated to contain more nutrients than they require. Hence, comparisons between lupins and other vegetable protein sources may be misleading. Despite this, there is evidence that lupins have a potential role in the nutrition of aquaculture species (Edwards & van Barneveld, 1998).

Robiana et al. (1995) examined the partial substitution of fishmeal with soyabean meal and lupin seed meal in diets for gilthead seabream (*Sparus aurata*). Mean feed intake and growth rate were not influenced by the type or level of plant protein in the diet. Feed conversion ratio and protein efficiency ratio were also unaffected. It is important to note that fish fed on lupin seed meal had reduced intestinal trypsin activities and a higher peak NH3 excretion rate, which appeared 2 h later than in the fish fed on diets containing fishmeal. These results, and the fact that gilthead seabream are essentially carnivores, are encouraging for the potential of lupins in aquaculture diets.

Lupin seed meal has also been assessed against pea meal and faba bean meal as a replacement for brown fishmeal in diets for rainbow trout (*Oncorhynchus mykiss*; Gouveia et al. 1993). All vegetable protein sources were included to provide 200 g of the dietary protein/kg diet. The fish fed on the vegetable protein sources performed better than those fed on the control diet with the best performance achieved with lupins. Gomes & Kaushik (1990) reported no effect on growth rates, feed conversion ratio or apparent digestibility coefficients when lupin seed meal provided 10 or 200 g of the dietary protein/kg diet. As lupins have a
higher protein content than peas and faba beans, they would have had the lowest inclusion level in the diets. Moyano et al. (1992) showed that rainbow trout diets containing 500 or 700 g lupins/kg diet supported growth rates, fish acceptance and nutritive utilization similar to fish fed on a whole fish-diet or a commercial trout feed. Further support for the use of lupins in rainbow trout diets has been provided by Hughes (1988, 1991). In contrast, Higuera et al. (1988) and Gomes & Kaushik (1990) reported that growth rate, feed conversion ratio and apparent digestibility coefficient were depressed when lupin seed meal provided more than 300 g of the protein/kg rainbow trout diet.

Lupins have also shown potential for use in diets for carp (Cyprinus carpio; Viola et al. 1988), pink snapper or red sea bream (Pagrus auratus; Jenkins et al. 1994) and marron (Cherax destructor; Morrissy, 1992; Tsvetnenko et al. 1995).

**Nutritional chemistry of lupins**

Overall, lupin seed holds great potential as a protein and energy source for livestock. Optimum use of lupins in livestock diets, however, will depend on our ability to understand the unique properties associated with the nutritional chemistry of lupins.

**Carbohydrate**

The carbohydrate chemistry of lupins is different to most legumes with negligible levels of starch and high levels (up to 500 g/kg seed; Miao, 1998) of soluble and insoluble NSP and oligosaccharides.

*Non-starch polysaccharide composition.* The content and chemical composition of lupin NSP varies between species and cultivars but their structures seem to be quite similar (Cheung, 1990). Lupins contain pectic substances with the major polysaccharide being β-(1-4)-galactan consisting of a mixture of D-galactose, L-arabinose, L-rhamnose, and galacturonic acid (Carre et al. 1985). A detailed conformation of the polysaccharide components of whole lupins, lupin kernel and lupin hulls was reported by van Barneveld (1997c; Table 2). There is proportionately more hemicellulose in the crude fibre component of lupins compared with legumes such as peas and faba beans which have cellulose as the major component of fibre (Table 3; Reddy et al. 1983; Bach Knudsen, 1997). The lignin content of lupins is also comparatively low although similar to levels observed in peas (Table 3).

*Non-starch polysaccharide digestion and utilization by livestock.* The high level of readily fermentable NSP in lupins has a significant effect on the way energy is derived from this legume by livestock. In single-stomached animals and ruminants, energy contained within monosaccharides absorbed from the small intestine is utilized differently from volatile fatty acids derived from fermentation taking place in the hindgut (or rumen in the case of ruminants). For ruminants, high levels of fermentable NSP and negligible levels of starch in lupins contribute to the high ME value (Margan, 1994). Typical ME contents of lupins for sheep are 12.2 MJ/kg (on an air-DM basis) for *L. angustifolius* and 12.5 for *L. albus* (Petterson et al. 1997) with rumen degradable protein ranging from 420 to 950 g/kg (Ørskov & Macdonald, 1992; Table 4).
Table 2. Carbohydrate composition (g/kg, air-DM basis) of whole seed, kernel and hulls of *L. angustifolius* cv Gungurru and *L. albus* cv Kiev mutant (van Barneveld, 1997c)

<table>
<thead>
<tr>
<th>Variable</th>
<th><em>L. angustifolius</em> cv Gungurru</th>
<th><em>L. albus</em> cv Kiev mutant</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Whole</td>
<td>Kernel</td>
</tr>
<tr>
<td>Free sugars</td>
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<tr>
<td>Rhamnose</td>
<td>0.09</td>
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</tr>
<tr>
<td>Xylose</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Mannose</td>
<td>0.05</td>
<td>0.05</td>
</tr>
<tr>
<td>Galactose</td>
<td>0.12</td>
<td>0.12</td>
</tr>
<tr>
<td>Glucose</td>
<td>0.06</td>
<td>0.06</td>
</tr>
<tr>
<td>Insoluble NSP</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rhamnose</td>
<td>0.02</td>
<td>0.02</td>
</tr>
<tr>
<td>Fucose</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Ribose</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Arabinose</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>Xylose</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Mannose</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
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<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Glucose</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Soluble NSP</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rhamnose</td>
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<td>0.00</td>
</tr>
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<td>0.00</td>
</tr>
<tr>
<td>Glucose</td>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>

NSP, non-starch polysaccharides.

Table 3. Comparative carbohydrate composition (g/kg DM) of vegetable protein sources commonly used in livestock diets

<table>
<thead>
<tr>
<th>Component</th>
<th>Soyabean meal</th>
<th>Peas</th>
<th>Faba beans</th>
<th>Lupins</th>
</tr>
</thead>
<tbody>
<tr>
<td>Starch</td>
<td>27</td>
<td>454</td>
<td>407</td>
<td>14</td>
</tr>
<tr>
<td>Cellulose</td>
<td>62</td>
<td>53</td>
<td>81</td>
<td>131</td>
</tr>
<tr>
<td>Hemicellulose</td>
<td>–</td>
<td>10–15</td>
<td>40–46</td>
<td>93–99</td>
</tr>
<tr>
<td>Total NSP</td>
<td>217</td>
<td>180</td>
<td>190</td>
<td>405</td>
</tr>
<tr>
<td>Klasson lignin</td>
<td>233</td>
<td>192</td>
<td>210</td>
<td>416</td>
</tr>
<tr>
<td>Dietary fibre</td>
<td>400</td>
<td>735</td>
<td>705</td>
<td>534</td>
</tr>
</tbody>
</table>

NSP, non-starch polysaccharide; CHO, carbohydrate.

Table 4. Typical nutrient content of lupins for ruminant livestock (as-is basis)*

<table>
<thead>
<tr>
<th></th>
<th><em>L. angustifolius</em></th>
<th><em>L. albus</em></th>
<th><em>L. luteus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>ME cattle (MJ/kg)</td>
<td>12.0</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>ME sheep (MJ/kg)</td>
<td>12.2</td>
<td>12.5</td>
<td>–</td>
</tr>
<tr>
<td>Rumen degradable protein (g/kg)</td>
<td>420–950</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

ME, metabolizable energy.

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<td>705</td>
<td>534</td>
</tr>
</tbody>
</table>

NSP, non-starch polysaccharide; CHO, carbohydrate.

* All data from Bach Knudsen (1997), except for hemicellulose (Reddy et al. 1983).

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<table>
<thead>
<tr>
<th></th>
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<td>–</td>
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<tr>
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<td>420–950</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

ME, metabolizable energy.

* From Petterson et al. (1997); Ørskov & Macdonald (1992).
The dominance of the carbohydrate profile by β-galactan (Carre et al. 1985), and the higher proportion of hemicellulose in the endosperm compared with cellulose in the hull, results in a fermentation pattern which is less rapid and less likely to lead to lactic acidosis. In contrast, when feed ingredients that contain a high proportion of hindgut fermentable carbohydrates, such as lupins, are fed to pigs, the digestible energy contribution often significantly over-estimates the net energy content (Taverner et al. 1983). Thus, the high NSP levels in lupins make it difficult to optimize the efficiency of lupin use in pig diets unless net energy measurements are made. As poultry lack any appreciable levels of hindgut fermentation, apparent ME measurements are good indicators of available energy and the energy contributions from lupins can be defined comparatively accurately before inclusion in diets.

Due to the low levels of starch and high levels of fermentable NSP, lupins can be fed freely as a supplement to grazing ruminants without the need for a period of introduction (Edwards & van Barneveld, 1998). Similarly in prepared mixes for dairy cows or feedlot cattle the replacement of cereal grain with lupins lowers the risk of acidosis, as well as providing additional protein. The use of high lupin levels in lieu of cereal grain in feedlot starter diets can facilitate the adaptation to high grain intakes without incurring the slower growth usually witnessed in the introductory period (Callow, 1987).

In pigs, van Barneveld et al. (1995) demonstrated that as the level of lupins increase in the diet, digestible energy does not change, but the proportion of energy digested by the end of the small intestine (which will influence net energy) significantly decreases. These findings may account for the high degree of variation that has previously been observed in the digestible energy content of ground whole lupin seed and lupin kernels. Wigan et al. (1994) reported a range of 12.3–15.3 MJ/kg for lupin seed meal and 15.4–16.6 MJ/kg for lupin kernels.

Given that DE is an inappropriate measure of energy availability from lupins used in pig diets, Noblet (1997) and Noblet et al. (1998) redefined the energy value of the ground whole seed and kernel of L. angustifolius and L. albus fed to growing pigs and adult sows. There was a vast difference in the DE measurements and net energy content of the ground whole seed and kernel of both species with the net energy content of L. albus superior to L. angustifolius (Table 5). Noblet et al. (1998) suggested that lupins are an excellent energy source for pigs in spite of their high rate of digestion in the hindgut. Their net energy values can also be estimated from general equations established from measurements on diets with the exception of L. angustifolius. Additional measurements on the metabolic effects of hulls from L. angustifolius suggested there was no difference in the net energy content of the lupin samples compared with soyabean.

Table 5. Energy values of the whole seed, kernel and hulls of L. angustifolius and L. albus in growing pigs (determined using the difference method) (Noblet, 1997)

<table>
<thead>
<tr>
<th></th>
<th>L. angustifolius</th>
<th>L. albus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Whole seed*</td>
<td>Kernel</td>
</tr>
<tr>
<td><strong>Energy values (MJ/kg DM)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ileal DE</td>
<td>10.94 (10.96)</td>
<td>13.04</td>
</tr>
<tr>
<td>Faecal DE</td>
<td>17.42 (17.05)</td>
<td>19.15</td>
</tr>
<tr>
<td>ME</td>
<td>16.51 (15.87)</td>
<td>17.64</td>
</tr>
<tr>
<td>NE (measured)</td>
<td>10.89</td>
<td>12.29</td>
</tr>
<tr>
<td>NE (estimated)†</td>
<td>10.79</td>
<td>12.19</td>
</tr>
</tbody>
</table>

DE, digestible energy; ME, metabolizable energy; NE, net energy.
* The values in parentheses are the energy value of seed calculated from addition of values obtained for kernel and hulls, according to their respective percentages in the seed.
† Estimated according to the equation NEg4 (Noblet et al. 1994).
The results of Noblet et al. (1998) demonstrate in pigs that the net energy content of the ground whole seed of lupins of either species (*L. angustifolius* and *L. albus*) is approximately 10.5 MJ/kg DM. In direct contrast to Wigan et al. (1994), comparison of the results of Noblet (1997; Table 6) with previous digestibility coefficients for energy in lupins (Bourdon et al. 1980; Aguilera et al. 1985) show that, irrespective of the origin of the samples and methods used for determination, the digestibility coefficient of energy in *L. albus* is relatively constant (0.83 on average). The variability is higher for *L. angustifolius*, yet this may be exaggerated by the fact that the only other reported values were generated by Fernandez & Batterham (1995) with sugar-based diets and consequently, significant differences in the NSP content of the experimental diets used in the two studies.

The sow has a high capacity for hindgut fermentation of lupin kernel and hulls and consequently can extract a significant amount of energy from lupins when they are included in diets (Table 6). Noblet (1997) reported that sows could extract 14.0 MJ of ME (DM basis) from lupin hulls compared with 7.4 MJ/kg DM by growing pigs. Not only does this result suggest that lupin hulls are highly fermentable, but it demonstrates the need for care when feeding lupins to sows. High fermentation levels are accompanied by high levels of gas production and if lupins are included in sow diets at levels above 200 g/kg diet the excess gas production can compromise their health.

Mullan & van Barneveld (1997) determined the DE content of *L. luteus* to be 16.41 MJ/kg (DM basis) in pigs. This is similar to the DE content of *L. albus* determined by King (1997). Jacyno et al. (1992a) estimated the ME content of *L. luteus* cv Topaz using regression equations described by Schiemann et al. (1971) to be 15.28 MJ/kg DM in pigs.

As stated previously, inclusion of *L. albus* in pig diets at levels above 100 g/kg diet results in significant reductions in growth performance, largely due to reductions in feed intake. In attempting to identify causes of reduced intake associated with feeding *L. albus*, Dunshea (1997) suggested that levels of Mn, methionine or alkaloids were all unlikely causes, but rather NSP composition or an unidentified anti-nutritional factor. To support this hypothesis, Dunshea (1997) examined the mean retention time of diets containing *L. angustifolius* and *L. albus*, respectively in pigs. Inclusion of *L. angustifolius* at 400 g/kg diet in a wheat-based (560 g/kg wheat) diet decreased mean retention time compared with wheat alone or wheat plus pea diets.

---

### Table 6. Comparative nutritional value of *L. angustifolius* fractions in diets fed to growing pigs and adult sows (Noblet, 1997)

<table>
<thead>
<tr>
<th>Digestibility coefficients</th>
<th>Whole seed</th>
<th>Kernel</th>
<th>Hulls</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grower*</td>
<td>Sow*</td>
<td>Grower</td>
<td>Sow</td>
</tr>
<tr>
<td>Organic matter</td>
<td>0.79</td>
<td>0.88</td>
<td>0.83</td>
</tr>
<tr>
<td>Crude protein</td>
<td>0.85</td>
<td>0.87</td>
<td>0.84</td>
</tr>
<tr>
<td>Ether extract</td>
<td>0.67</td>
<td>0.64</td>
<td>0.67</td>
</tr>
<tr>
<td>Crude fibre</td>
<td>0.43</td>
<td>0.91</td>
<td>0.48</td>
</tr>
<tr>
<td>Nitrogen-free extract</td>
<td>0.89</td>
<td>0.91</td>
<td>0.93</td>
</tr>
<tr>
<td>Energy</td>
<td>0.77</td>
<td>0.85</td>
<td>0.81</td>
</tr>
</tbody>
</table>

#### Energy values (MJ/kg DM)
- ME/DE (%): Grower 93.9 Sow 94.0 Grower 92.4 Sow 92.4 Grower 101.4 Sow 99.0

ME, metabolizable energy; DE, digestible energy.
* The values in parentheses are the energy value of seed calculated from addition of values obtained for kernel and hulls, according to their respective percentages in the seed.
However, when included at 350 g/kg in diets containing animal protein supplements in addition to wheat (470 g/kg) there was no effect on retention time. These findings suggest that there may be some interaction between the *L. angustifolius* and wheat at high inclusion rates but not at lower inclusion rates. On the other hand, inclusion of *L. albus* consistently increased mean retention time when included at 350 or 400 g/kg diet and whether as either ground whole seed or kernels. A strong inverse relationship between feed intake and retention time supports the hypothesis that the reduction in feed intake observed in pigs consuming diets containing *L. albus* is due to an increase in retention time through delayed digestion and fermentation in the hindgut. However, slaughter data suggest that the actual site of delay in retention may be the stomach rather than the hindgut, although the latter cannot be discounted. Delay in the stomach may affect VFI through feedback on satiety signals (Dunshea, 1997).

Hughes *et al.* (1998) reported the effects of species and cultivar of lupins on the apparent ME content for broiler chickens (Table 7). Samples of *L. albus* cv Kiev mutant exhibited a significantly higher energy value (11.59–13.29 MJ/kg DM) and more efficient growth than samples of *L. angustifolius* cv Danja or Gungurru. Apparent ME values for these cultivars were not significantly different and ranged from 8.24 to 11.00 MJ/kg DM with the exception of a single sample of Danja, which had an apparent ME of 6.53 MJ/kg DM. Similarly high apparent ME estimates for lupins were reported by Annison *et al.* (1994) who examined the influence of lupin inclusion level on apparent ME estimates. Inclusion of lupins at levels of 100, 200 and 300 g/kg diet, respectively, in a sorghum + casein basal diet resulted in an apparent ME estimate of 10.26 MJ/kg DM. There was no indication of anti-nutrients affecting energy metabolizability being present in lupins.

The results of Hughes *et al.* (1998) are somewhat higher than previously reported lupin apparent ME values for poultry. Johnson & Eason (1991) reported the apparent ME of Victorian and Western Australian lupins to be 9.6 and 7.2 MJ/kg DM, respectively, while Bryden *et al.* (1994) reported the apparent ME of lupin seed meal to be 8.66 MJ/kg DM. Differences in reported apparent ME estimates may be due to experimental variation or differences in the samples of lupins tested. In general, the apparent ME of lupins is inferior to other grain legumes such as peas (10.8 MJ/kg DM), faba beans (11.0 MJ/kg DM) and vetch (10.8 MJ/kg DM), possibly due to the absence of any appreciable hindgut recovery of energy through fermentation.

The apparent ME of *L. luteus* was determined by Hughes *et al.* (1998) to be 11.4 MJ/kg DM. *L. luteus* also supported high growth rates in broiler chickens and appears to have a nutritional value superior to *L. angustifolius* but similar to *L. albus* in terms of growth, feed conversion, apparent ME and ileal viscosity. *L. luteus* had much the same influence on excreta moisture as *L. angustifolius* and *L. albus*.

Table 7. Effects of species and cultivar of lupin on the apparent metabolizable energy (ME) and excreta moisture content when fed to broiler chickens (Hughes *et al.* 1998)

<table>
<thead>
<tr>
<th>Source</th>
<th>Species</th>
<th>Cultivar</th>
<th>Apparent ME (MJ/kg DM)</th>
<th>Excreta moisture (g/kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Merriden</td>
<td><em>L. angustifolius</em></td>
<td>Gungurru</td>
<td>8.76</td>
<td>740</td>
</tr>
<tr>
<td>Shackley</td>
<td><em>L. angustifolius</em></td>
<td>Gungurru</td>
<td>8.63</td>
<td>770</td>
</tr>
<tr>
<td>Chapman</td>
<td><em>L. angustifolius</em></td>
<td>Gungurru</td>
<td>8.58</td>
<td>740</td>
</tr>
<tr>
<td>Badgingarra</td>
<td><em>L. angustifolius</em></td>
<td>Gungurru</td>
<td>8.24</td>
<td>770</td>
</tr>
<tr>
<td>Henderson</td>
<td><em>L. angustifolius</em></td>
<td>Gungurru</td>
<td>8.53</td>
<td>760</td>
</tr>
<tr>
<td>Kattaning</td>
<td><em>L. angustifolius</em></td>
<td>Danja</td>
<td>8.25</td>
<td>760</td>
</tr>
<tr>
<td>Unknown</td>
<td><em>L. albus</em></td>
<td>Kiev mutant</td>
<td>11.59</td>
<td>740</td>
</tr>
<tr>
<td>Avondale</td>
<td><em>L. angustifolius</em></td>
<td>Gungurru</td>
<td>11.00</td>
<td>–</td>
</tr>
<tr>
<td>Hyden</td>
<td><em>L. angustifolius</em></td>
<td>Danja</td>
<td>10.45</td>
<td>–</td>
</tr>
<tr>
<td>Unknown</td>
<td><em>L. albus</em></td>
<td>Kiev mutant</td>
<td>13.29</td>
<td>–</td>
</tr>
</tbody>
</table>
The role of lupin NSP in poultry nutrition is by no means clear. Enzyme supplementation of cereal-based poultry diets is a common commercial practice with significant improvements in the yield of energy from diets and reduction in bird variability. The benefits of including enzymes in diets containing lupins still requires investigation, however, as does improved understanding of the role of lupin NSP and more specific targeting of supplementary enzymes. Positive production responses from the addition of supplementary enzymes to poultry diets containing lupins have been reported by Marquardt (1993), Brenes et al. (1993), Roth Maier & Kirchgessner (1994, 1995) and Annison et al. (1996), while no effect or a negative effect has been reported by Alloui et al. (1994), Annison et al. (1996), Roth Maier & Kirchgessner (1995) and Eder et al. (1996).

Oligosaccharides. Lupin seeds contain significant levels of oligosaccharides of the raffinose family (Steggerda et al. 1970; van Kempen et al. 1994; Table 8). These oligosaccharides appear to be indigestible in the stomach and the small intestine of the single-stomached animal due to a lack of α-galactosidase (EC 3.2.1.23) in the intestinal mucosa (Carre et al. 1985). However, bacteria in the lower intestinal tract are able to metabolize these sugars to CO₂, H₂ and CH₄. Total α-galactosides in different lupin species range from 70 to 120 g/kg DM (Trugo & Almeida, 1988). Stachyose is always reported as the main sugar in lupin seeds, accounting for up to 50% of the total sugars (van Kempen et al. 1994).

High levels of raffinose oligosaccharides may have a number of negative effects on the nutritional value of lupins. These may include (1) interference with the digestion of other nutrients in the small intestine; (2) decreased dietary net energy contributions due to a higher proportion of hindgut fermentation (Taverner et al. 1983; van Barneveld et al. 1995); (3) anaerobic fermentation of these sugars in the hindgut resulting in increased gas production; and (4) an osmotic effect of these oligosaccharides in the small intestine.

Extraction of oligosaccharides from lupins has been shown to improve the DE content for growing pigs (van Barneveld et al. 1996). An ethanol extraction process (Coon et al. 1990) removed 730 and 670 g/kg of the oligosaccharides from L. angustifolius and L. albus, respectively, but did not change the gross energy content. Ethanol extraction improved the DE of diets containing L. angustifolius and L. albus by 0.5 and 0.7 MJ/kg, respectively.

van Barneveld et al. (1997c) examined the influence of ethanol extraction on lupins to reduce the effect of the oligosaccharide content on the apparent ileal digestibility of amino acids in pigs. Ethanol extraction significantly improved (P<0.05) the digestion of all amino acids in both L. angustifolius and L. albus. Amino acid digestibility coefficients for L. angustifolius were increased by 0.05–0.10, while coefficients for L. albus were increased by 0.05–0.08 (Table 9). These results suggest that oligosaccharides are hindering the digestion of amino acids in the small intestine of pigs fed on diets containing lupins. This is in contrast to the findings of Gabert et al. (1995) and Zuo et al. (1996) and suggests that the properties of lupin oligosaccharides may differ from soyabean-meal oligosaccharides and oligosaccharide isolates. The results also demonstrate that the increase in lupin DE consistent with oligosaccharide
extraction observed by van Barneveld et al. (1996) was due to more than a DE dilution when oligosaccharides were present.

Unlike pigs, the presence of high levels of raffinose oligosaccharides from lupins does not appear to influence the digestion of nutrients by poultry, despite suggestions to the contrary (Marquardt, 1993). In fact, removal of oligosaccharides from legumes or oilseed meals may even depress poultry performance.

Hughes et al. (1998) examined the effects of dietary addition of ethanol-extracted lupin kernel on apparent ME and growth performance of chickens. Samples of *L. angustifolius* cv Gungurru or Danja were fed at levels of up to 300 g/kg diet in a semi-purified diet to poultry as either raw kernel or following ethanol extraction to remove oligosaccharides. Removal of oligosaccharides by ethanol extraction resulted in significantly reduced apparent ME and performance of chickens given diets containing 300 g *L. angustifolius* cv Gungurru or Danja/kg diet (Table 10). Viscosity of ileal digesta was doubled as a result of the ethanol extraction process, whereas moisture content of the excreta was unaffected. Similar results were reported by Irish et al. (1995) when α-galactosides of sucrose were removed from soyabean meal using ethanol extraction. Hence, in contrast to the suggestions of Marquardt (1993), oligosaccharides in lupins actually appear to contribute to the apparent ME content and should not be regarded as having anti-nutritive effects on poultry diets.

To further support the differences in the utilization of oligosaccharides between pigs and poultry, Hughes et al. (1998) used the same lupin samples and diets as van Barneveld et al. (1997c) to compare the response obtained in poultry with pigs. Ethanol extraction, and subsequent reduction in the oligosaccharide content (and possibly other compounds) of *L. angustifolius* cv Gungurru kernel, resulted in a significant decline in apparent ME and DM digestibility when the diets were fed to poultry. There was no significant effect observed when *L. albus* cv Kiev mutant kernel was fed following ethanol extraction, yet in pigs, ethanol extraction of this lupin resulted in the greatest improvement in amino acid and energy digestion. This may help explain some of the differences in the ability of pigs and poultry to utilize *L. albus*.

### Proteins and amino acids

**Protein composition.** The protein content of legumes can be variable. Petterson et al. (1997) reported significant variation in the crude protein content of individual batches of *L. angustifolius* (272–372 g/kg, air-DM basis) and *L. albus* (291–403 g/kg, air-DM basis). However, the crude protein content of mixed samples of lupins released from bulk-handling authorities

<table>
<thead>
<tr>
<th>Table 9. Ileal digestibility coefficients for some essential amino acids in untreated and ethanol extracted dehulled <em>L. angustifolius</em> and <em>L. albus</em> fed to growing pigs (van Barneveld et al. 1997c)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment . . .</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>Threonine</td>
</tr>
<tr>
<td>Valine</td>
</tr>
<tr>
<td>Isoleucine</td>
</tr>
<tr>
<td>Leucine</td>
</tr>
<tr>
<td>Phenylalanine</td>
</tr>
<tr>
<td>Lysine</td>
</tr>
<tr>
<td>Histidine</td>
</tr>
</tbody>
</table>

*ab Values within the same row with unlike superscript letters were significantly different (P<0.05).*
Table 10. Effects of dietary addition of ethanol-extracted lupin kernel on apparent metabolizable energy (ME) and growth performance of chickens (Hughes et al. 1998)

(Mean values and standard deviations)

<table>
<thead>
<tr>
<th>Sample</th>
<th>Ethanol extraction</th>
<th>Feed conversion ratio (g feed/g gain)</th>
<th>Growth rate (g/bird per 24–31 d)</th>
<th>Apparent ME of diet (MJ/kg DM)</th>
<th>Ileal viscosity (cP)</th>
<th>Excreta moisture (g/100 g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sorghum (control)</td>
<td>–</td>
<td>2.12a 0.09</td>
<td>378b 22</td>
<td>15.4a 0.2</td>
<td>3.0c 0.6</td>
<td>570c 40</td>
</tr>
<tr>
<td>L. angustifolius cv Gungurru</td>
<td>No</td>
<td>2.01a 0.08</td>
<td>429a 18</td>
<td>13.8b 0.3</td>
<td>6.8c 4.0</td>
<td>730a 20</td>
</tr>
<tr>
<td>L. angustifolius cv Gungurru</td>
<td>Yes</td>
<td>2.15a 0.25</td>
<td>376b 52</td>
<td>13.0c 0.3</td>
<td>15.2bc 10.2</td>
<td>740b 30</td>
</tr>
<tr>
<td>L. angustifolius cv Danja</td>
<td>No</td>
<td>2.04a 0.06</td>
<td>420a 34</td>
<td>13.4bc 0.3</td>
<td>8.4bc 3.0</td>
<td>740a 30</td>
</tr>
<tr>
<td>L. angustifolius cv Danja</td>
<td>Yes</td>
<td>2.13a 0.19</td>
<td>378b 43</td>
<td>12.6c 0.6</td>
<td>17.6a 7.0</td>
<td>740a 30</td>
</tr>
</tbody>
</table>

a,b,c Values in a column with unlike superscript letters were significantly different ($P<0.05$).
is remarkably consistent (M Tucek, Grain Pool of Western Australia, personal communication).

The structure of lupin proteins gives them unique physicochemical properties. The storage proteins are mainly composed of globulins, with this fraction being higher in lupins and soyabeans than most other legumes (Table 11; Adsule & Kadam, 1989). The globulins themselves are composed of two major proteins characterized by their sedimentation coefficient, which in most cases approaches 7S and 11S. These storage proteins are multimeric and readily undergo association and dissociation reactions, allowing their efficient packing within the protein body in an insoluble form (Adsule & Kadam, 1989). The ratio of these globulin proteins affects the behaviour of lupin proteins and makes them different from other legume species (Gueguen, 1983). In lupin proteins the 7S-like protein is found in larger proportions than the 11S-like protein, the 7S : 11S ratio being about 1:3 : 1 (Table 11). The 11S or legumin type protein in Lupinus spp. has been identified as γ-conglutinin (Mironenko et al. 1978). Similarly, soyabean has a 7S : 11S ratio of 1:6 : 1 (Thank & Shibasaki, 1976). In contrast, faba beans and peas have legumin as the major protein with a 7S : 11S (vicilin to legumin) ratio close to 1 : 2 (Table 11).

A knowledge of the major fractions of lupin proteins allows us to develop a profile of their functional properties and potential nutritional influences. The fact that lupin storage proteins are predominantly globulins suggests that they probably have poorer emulsion properties (i.e. lower solubility) than a legume with higher levels of albumins (such as French beans; Sathe & Salunkhe, 1981). Higher levels of globulins would also suggest that lupin proteins are less viscous than legume proteins dominated by albumins, and as globulins have a compact structure, lupin proteins may have a lower buffering capacity in the neutral pH range. This is likely to be due to the hydrophilic groups on these proteins remaining buried in the interior of the molecule, thus not being exposed under neutral pH (Satterlee et al. 1975).

Amino acid composition. While it is recognized that the balance of amino acids in a feed ingredient does not have to exactly match the requirements of the target species, as any deficiencies can be met by other diet ingredients, the closer the match between the amino acid profile of the ingredient and the animal’s requirements, the higher the comparative nutritional value of that feed ingredient. For single-stomached animals, we can see that lupins are particularly poor sources of methionine (0·59–0·87 g/16 g N) and lysine (4·21–5·21 g/16 g N). In contrast, lupins supply excessive levels of arginine to the diet (10·6–13·5 g/16 g N). With the exception of lysine, Gatel (1994) suggested that these characteristics of lupins make them ideal complements to cereals (very low levels of lysine and a higher proportion of sulfur amino acids) in single-stomached animals’ diets. Thus from a diet formulation perspective, lupins are a valuable resource.

### Table 11. Comparison of protein components in common legumes (Gueguen, 1983)

<table>
<thead>
<tr>
<th>Legume</th>
<th>Albumin</th>
<th>Globulin</th>
<th>Glutelins</th>
<th>Vicilin : legumin ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Faba beans</td>
<td>20</td>
<td>60</td>
<td>15</td>
<td>1:6:1:7</td>
</tr>
<tr>
<td>Peas</td>
<td>21</td>
<td>66</td>
<td>12</td>
<td>1:3:4:2</td>
</tr>
<tr>
<td>Soyabean</td>
<td>10</td>
<td>90</td>
<td>0</td>
<td>1:6:1</td>
</tr>
<tr>
<td>Dry beans</td>
<td>15</td>
<td>75</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>Lupin seeds</td>
<td>10–20</td>
<td>80–90</td>
<td>0</td>
<td>1:3:1</td>
</tr>
</tbody>
</table>
Edwards & van Barneveld (1998) presented the amino acid supply of lupins relative to that of rumen bacterial protein and the ‘ideal’ amino acid profile for post-duodenally absorbed protein for high producing dairy cows (Table 12). As for single-stomached animals, lupins are poor suppliers of methionine relative to other amino acids for ruminants, and contribute excessive amounts of arginine. There is also the question of whether the amino acid profile of that proportion of lupin protein that escapes rumen degradation differs from that of the original material, and in fact is markedly inferior to the protein as fed (Mathers et al. 1979). If coarsely ground lupins are incorporated as part of a high-feeding level for high producing cows, there may be a greater proportion of the protein which escapes rumen degradation than at a maintenance level of feeding. Yet when lupins have been compared with other protein sources in situations likely to respond to by-pass protein, they have been found inferior to other protein sources (Lemerle et al. 1985).

The comparatively low level of sulfur amino acids in lupins can be compensated for by methionine contributions from other diet ingredients or by dietary supplementation with synthetic methionine when feeding ruminants or single-stomached animals. The comparatively high levels of arginine are cause for concern when feeding lupins to livestock as arginine and lysine are antagonists and compete for a common carrier at cell level (van Barneveld, 1997a).

In practice, however, the high arginine levels do not appear to affect lysine availability in lupins as demonstrated in pigs by van Barneveld (1997a) who induced a dietary arginine imbalance of

<table>
<thead>
<tr>
<th>Amino acid</th>
<th>L. angustifolius*</th>
<th>L. albus*</th>
<th>Rumen bacterial protein†</th>
<th>Ideal protein‡</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lysine</td>
<td>4.66</td>
<td>4.20</td>
<td>8.0</td>
<td>100</td>
</tr>
<tr>
<td>Methionine</td>
<td>0.72</td>
<td>0.65</td>
<td>2.5</td>
<td>31</td>
</tr>
<tr>
<td>(Cystine)</td>
<td>1.48</td>
<td>1.30</td>
<td>5.8</td>
<td>73</td>
</tr>
<tr>
<td>Threonine</td>
<td>3.36</td>
<td>3.13</td>
<td>3.8</td>
<td>73</td>
</tr>
<tr>
<td>Isoleucine</td>
<td>3.97</td>
<td>3.72</td>
<td>5.9</td>
<td>74</td>
</tr>
<tr>
<td>Tryptophan</td>
<td>1.06</td>
<td>0.97</td>
<td>4.9</td>
<td>61</td>
</tr>
<tr>
<td>Arginine</td>
<td>12.03</td>
<td>12.44</td>
<td>7.7</td>
<td>96</td>
</tr>
<tr>
<td>Leucine</td>
<td>3.97</td>
<td>6.06</td>
<td>7.7</td>
<td>103</td>
</tr>
<tr>
<td>Valine</td>
<td>3.91</td>
<td>3.64</td>
<td>6.2</td>
<td>78</td>
</tr>
<tr>
<td>Histidine</td>
<td>2.41</td>
<td>1.72</td>
<td>1.8</td>
<td>23</td>
</tr>
<tr>
<td>Phenylalanine</td>
<td>3.65</td>
<td>3.27</td>
<td>5.3</td>
<td>66</td>
</tr>
</tbody>
</table>

RL, relative to lysine.
* Data from Pettersen et al. (1997).
† Data from Rulquin & Verité (1993).
‡ Data from Chalupa & Sniffen (1993).

Table 13. Response of growing pigs, fed on diets containing soyabean meal at 3-3× maintenance energy requirement, to added dietary arginine (van Barneveld, 1997a)

<table>
<thead>
<tr>
<th>Diet</th>
<th>3-3× maintenance energy requirement</th>
<th>3-3× maintenance energy requirement + arginine</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P</td>
<td>SEM</td>
</tr>
<tr>
<td>Daily gain (g)</td>
<td>748</td>
<td>2.02</td>
</tr>
<tr>
<td>Feed conversion ratio</td>
<td>2.16</td>
<td>0.075</td>
</tr>
</tbody>
</table>

Table 12. Essential amino acid profile of lupin protein, rumen bacterial protein and ideal amino acid balance in post-duodenally absorbed protein for high producing dairy cows (Edwards & van Barneveld, 1998)
2.45:1 (i.e. similar to the imbalance in lupins) in a soya bean meal-based diet fed at 3.3×maintenance. This imbalance did not result in a significantly different growth response (Table 13).

It should also be noted that more recently domesticated species of lupins, such as L. luteus, have lysine, threonine, cystine and methionine concentrations that are significantly higher than the more traditional varieties (Mullan et al. 1997). These species show great potential as livestock feeds and have protein levels comparable to soya bean meal if offered dehulled.

**Nutritional characteristics of lupin proteins and amino acids.** The degree of protein degradation in the rumen varies from 42 to 95%, based on work by Ørskov & McDonald (1979), using a synthetic-fibre bag technique. The lower levels of rumen protein degradation were associated with ground whole seed at high fractional outflow rates (high feeding levels), while the high degradation rates (low by-pass values) were associated with fine grinding and/or low fractional outflow rates (low level feeding). Dixon & Hosking (1992) suggest that most studies of ruminant degradability of lupins under practical conditions report high degradation rates of 800 g/kg or more. Although the method of seed preparation can influence the proportion of lupin protein that ‘by-passes’ rumen fermentation, in most instances the proportion of lupin protein and amino acids that reach the abomasum intact is quite low (Dixon & Hosking, 1992; Margan, 1994).

The availability of amino acids in lupin fed to pigs is high. van Barneveld et al. (1997a) utilized a modified slope-ratio analysis of a growth experiment to redefine the availability of lysine in lupins. This modified methodology involved varying the lysine intake of pigs by varying daily feed intake rather than the concentration of lupins in the experimental diets. This approach eliminated any interactions between NSP from the various diet components that may have been accelerated as the dietary inclusion of lupins increased. This phenomenon may have contributed to the low results reported by Batterham et al. (1984). van Barneveld et al. (1997a) recommended the following lupin lysine availability values for use when formulating diets for pigs: L. angustifolius (ground whole seed), 0-75; L. angustifolius (kernel), 0-72–0-75; L. albus (ground whole seed), 0-67; L. albus (kernel), 0-76. These results are supported by the results of Godfrey & Payne (1987). The differences between the results achieved by Batterham et al. (1984) and van Barneveld et al. (1997a) may also have been due to differences in the cultivars tested.

There is good agreement between the apparent ileal digestibility of lysine and the availability of lysine in L. angustifolius and L. albus (van Barneveld, 1997a). This result suggests the apparent ileal digestibility of other amino acids in lupins can be used as a reasonable measure of availability when formulating diets. The apparent ileal digestibility of amino acids in L. luteus is particularly high with no significant difference between this lupin and soya bean meal (Mullan & van Barneveld, 1997). Without direct comparison, the ileal digestibility of amino acids in the ground whole seed of L. luteus in many cases also appears to be equivalent to, or higher than, the apparent ileal digestibility of amino acids in the ground whole seed of L. angustifolius and L. albus.

Published data suggest that the digestibility and availability of amino acids in lupins for poultry is high. In a comparative study between pigs, rats and chicks, the availability of lysine in three samples of lupin seed meal determined using slope-ratio analysis was shown to be high for poultry (Batterham, 1992), ranging from 0.84 to 0.98. Although comparable to the values determined for rats, the availability of lysine in these samples of lupin seed meal was shown to be significantly higher in poultry than pigs. Ravindran et al. (1998) reported that the apparent ileal digestibility coefficients of all amino acids in both L. angustifolius and L. albus exceeded 0-73, with most well above 0-80. Rhone Poulenc Animal Nutrition (1989) reported a true protein digestibility coefficient of 0.95 for lupins determined using caecectomized poultry
compared with 0.90 for field peas and 0.90 for full-fat soyabeans. Amino acid digestibility coefficients for lupins ranged from 0.91 for lysine up to 0.97 for arginine, glycine, leucine and tyrosine. Similar results for lupin seed meal were reported by Heartland Lysine Inc. (1992).

Robiana et al. (1995) reported apparent protein digestibility coefficients in fish of 0.96, 0.95 and 0.93 for diets containing 100, 200 or 300 g lupin seed meal/kg, respectively. Similarly, the digestibility of N in lupin has been shown to be extremely high when fed to silver perch (G Allan, unpublished results). The methodology used to determine these digestibility coefficients may, however, be artificially elevating the values, resulting in lower than expected subsequent growth performance.

**Lipids**

The crude fat content of lupins varies within and between species: typical values for common species grown in Australia include (g/kg): L. albus 86±8–130±0, L. angustifolius 49±4–69±7, L. atlanticus 13±0–46±0, L. consentinii 27±0–41±6, L. luteus 52±0–61±0 (Petterson et al. 1997). Hansen & Czochanska (1974) extracted total lipids from whole L. angustifolius seeds and found they comprised (g/kg): triacylglycerols 711, phospholipids 149, free sterols 52, glycolipids 35, sterol and wax esters 5, free alcohols 4, hydrocarbons 4, unidentified waxy material 4. The main fatty acids present were (g/kg): linoleic 483, oleic 312, palmitic 76, linolenic 54. Seed coatings constituted 239 g/kg of the whole seeds and contained 1±5% of the lipids. Petterson (1998) reported that extracts of L. angustifolius oil were stable for 3 months at 51°C indicating a high level of antioxidant activity in this material.

Nutritionally, the lipid content and composition of lupins will influence livestock production by affecting DE and ME contributions to the diet. In pigs, the level of supplementary fat could influence DE contributions from lupins, particularly if L. albus or L. luteus are fed, depending on saturated:unsaturated fatty acid ratio (Stahly, 1984). Lipid levels in lupins are unlikely to affect rumen fermentation patterns.

**Minerals**

A number of studies have investigated the potential for mineral components of lupins to influence livestock production, particularly in relation to the differences in performance between pigs fed L. angustifolius and L. albus. For example, L. albus is a Mn accumulator and it has been suggested that high Mn may reduce VFI. King (1981) fed barley-based diets containing 270 g/kg soyabeans meal, 330 g/kg L. albus seed meal or 330 g/kg L. angustifolius seed meal to grower pigs. These diets contained 43, 750 and 72 μg Mn/kg respectively. The L. angustifolius diet was then supplemented with 210–1260 μg Mn/kg. VFI and daily gain were reduced on feeding both basal lupin-seed meals and there was no further effect of increasing levels of Mn. More recently, researchers at Washington State University, WA, USA have confirmed that inclusion of Mn into control diets (soyabean) to the same level as that seen in L. albus diets had no effect on feed intake, whereas L. albus inclusion reduced VFI in a dose-dependent manner (Dunshea, 1997). Therefore, excessive Mn levels in lupins do not appear to be the cause of reduced VFI.

L. luteus appears to extract greater concentrations of some minerals from the soil, most notably, Cd (W Cowling, unpublished results). However, it would appear unlikely that the
levels in the lupins used by Mullan et al. (1997) were high enough to influence their nutritional value adversely.

The availability coefficients of P in lupins has been estimated to be 0.53, compared with 1.00 from an inorganic P standard, on the basis of tibia bone-breaking strength (Antoniewicz et al. 1992). Despite some reports of increased incidence of leg weakness with increasing dietary levels of lupins, Centeno et al. (1990) observed no effects of supplementation with up to 400 g lupins/kg diet on the concentrations of plasma minerals in broiler chicks up to 4 weeks of age.

Anti-nutritional compounds

**Alkaloids.** While pigs are known to be sensitive to the presence of alkaloids in diets (e.g. Pearson & Carr, 1977), the average alkaloid content of current varieties of *L. angustifolius* and *L. albus* is generally low (<0.04 g/kg), although under certain conditions it can be higher. For example, in 1981–82 the average alkaloid content for lupins grown in Western Australia was 0.4 g/kg (range 0.3–1.3 g/kg) and several cases of feed rejection and vomiting in commercial piggeries were investigated. These cases were found to be caused by diets containing *L. angustifolius* with unusually high contents of alkaloid, resulting in total dietary alkaloid levels of 0.3–0.4 g/kg (AR Mercy and Y Emms, unpublished results). The higher values were attributed to lupins grown on infertile grey sands, deficient in Mn and K, and where yields of later maturing cultivars were low due to a dry finish to the season. Individual samples of lupins are of particular concern if these form the only source of lupins for pig diets, as is the case when home-mixers and feed manufacturers source their lupin supplies directly from growers. For this reason it is considered necessary to continue to monitor alkaloid levels in lupins, especially with respect to new varieties and the environment in which they have been grown.

The alkaloid content of the *L. albus* exhibits less variation within individual cultivars than do the *L. angustifolius* cultivars, and the overall alkaloid content of the former species is considerably lower (Harris et al. 1986). Therefore we can conclude that alkaloids are not the reason for the poor acceptance of *L. albus* by pigs.

Poultry appear far less sensitive to the presence of alkaloids in lupins compared with pigs. Buraczewska et al. (1993) included seeds of different lupins species (*L. albus*, *L. angustifolius* and *L. luteus*) with a known total alkaloid content (range 230–1300 mg/kg) in diets for pigs (100 or 140 g dietary protein only from lupins/kg diet) and for chickens (150 and 300 g lupins/kg balanced diet). Pigs were the most sensitive to alkaloids of *L. albus* with the tolerated concentration being below 120 mg/kg diet. In contrast, 3-week observations of feed intake by chickens revealed no negative correlation between intake of the diets and their alkaloid content.

**Saponins.** Saponins are glycosides present in many plants. They are characterized by their bitter taste and their anti-nutritional effect seems to be related to an increase of the permeability of the small intestinal mucosa cells. This leads to an inhibition of active nutrient transport but facilitates the uptake of materials that would not normally be able to permeate the gut (Johnson et al. 1986). Of the three saponins that have been identified in *L. angustifolius* one appears to have a novel structure (Ruiz et al. 1993) and the consequence of this needs further investigation.

It was thought that saponin levels in *L. albus* may be a factor responsible for poor feed intake by pigs fed on diets containing these lupins. Studies by RG Ruiz and DS Petterson (unpublished results) indicate that the level of saponins in *L. albus* is below that which is
analytically detectable, while the level in *L. angustifolius* ranged from 379 to 743 mg/kg. Cuadrado *et al.* (1995) also reported levels of saponins in *L. albus* of less than 12 mg/kg, whereas samples of *L. luteus* contained 55 mg total saponins/kg. This compared to 230–390 mg total saponins/kg in a range of bitter lupins (*L. mutabilis*). It was concluded by Cuadrado *et al.* (1995) that saponin contents were positively correlated with the alkaloid content of lupins. Based on the above data, it is unlikely that saponins are responsible for reduced feed intakes when *L. albus* is fed to pigs.

**Tannins.** While piglets are more sensitive to tannins than chickens, the levels in *L. angustifolius* are considered to be low enough for this not to be a problem in pig diets. However, there are very limited data on the tannin levels (total and condensed) in *L. albus* and *L. luteus* and this warrants further attention.

**Other compounds.** It has been reported that low-alkaloid lupins are also free of other anti-nutritional compounds such as trypsin inhibitors and haemagglutinins (Schoeneberger *et al.* 1983).

**Conclusions**

Lupin seed can be cost-effectively integrated into the diets of ruminant and single-stomached animals. Despite some characteristics of lupins favouring use in ruminant diets (such as negligible levels of starch, but high levels of fermentable NSP substrate), while others make them more suited for use in single-stomached-animals’ diets (e.g. highly digestible protein and amino acids), a knowledge of these characteristics and how to manipulate them ensures lupins can be used effectively by all livestock in their current form. Any plant breeding exercise or genetic engineering of lupins should focus only on improved yields under a wider range of growing environments. Further research is required to establish the underlying mechanisms for differences in the utilization of different species of lupins and to identify target sites for exogenous enzyme supplements. Additional information is also required on the nutritional role of lupin oligosaccharides and their potential for use in other systems.

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Nutritional quality of lupins for livestock


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