Genetic Associations of Growth and Feed Intake with Other Economically Important Traits in Pigs

J.P. Bidanel[*], P. Sellier[*] and H. Gilbert[*]

Introduction

Growth and feed intake are key biological functions in all livestock species. They largely contribute to the economic efficiency of production systems, particularly for meat production. Growth and development also determine the entire life of animals, from their survival early in life to the length and the quality of their (re)productive career. Feed intake is associated with many different aspects of livestock production such as the efficiency of feed utilization, competition for food, resource allocation, animal welfare or environmental impact. Both traits are thus major components of the breeding goal in meat producing species. It is therefore essential to have a precise idea of the genetic associations of daily weight gain and feed intake of the growing animal with other economically important traits in order to be able to draw a global picture of the consequences of selection for these two traits. The main objective of this paper is to review genetic correlations (r_g) of growth rate and feed intake/efficiency with other major traits in order to assess the potential consequences of selection for these traits in pigs.

Genetic parameters of growth, feed intake and feed efficiency

As in all mammalian species, the genetic variation of fetal and birth to weaning piglet growth is controlled by both piglet and dam genotypes, with a small to moderate antagonism between direct and maternal genetic effects (Roehe, 1999; Solanes et al., 2004; Rosendo et al., 2007). Maternal effects gradually decrease after weaning and can often be neglected during the fattening period. Direct heritability values for postweaning growth rate are moderate (0.3 on average - Clutter and Brascamp, 1998). Estimates of genetic correlations between early and late growth are not numerous in the literature. Solanes et al. (2004) reported positive direct and maternal genetic correlations between birth or weaning weight and postweaning growth, in agreement with the positive correlative response for birth weight to selection for lean growth rate (Kerr and Cameron, 1995). Conversely, Zhang et al. (2000) reported low or negative genetic correlations between weaning weight and days on test in a Chinese x European composite line. Although precise genetic parameter estimates are lacking in the literature, selection for growth and leanness has been shown to significantly increase mature size, with consequences on various aspects of pig production such as nutrient requirements or building design (Whittemore, 1994).

---

[*] INRA, UMR1313 Génétique Animale et Biologie Intégrative, F-78350 Jouy-en-Josas, France

No genetic parameter estimate for preweaning feed intake is, to our knowledge, available in the literature, but it can be hypothesized that direct effects (suckling activity) and maternal effects (milk supply) both contribute to the genetic variation of feed intake during the suckling period. Additive genetic effects for feed intake are essentially of direct origin during the fattening period, with moderate heritability values (0.20 to 0.51 - Labroue et al., 1997; Clutter and Brascamp, 1998; Gilbert et al., 2007; Cai et al., 2008);.

Genetic correlations between growth and feed intake during the fattening period are strongly positive on *ad libitum* feeding (Labroue, 1995; Clutter and Brascamp, 1998). Daily feed intake shows moderate positive genetic correlations with feed conversion ratio (0.29 – average of 16 estimates), but with quite variable values – from close to zero estimates (Von Felde et al., 1996; Labroue et al., 1997) to strongly positive ones (McPhee et al., 1979; Cameron et al., 1988). It has conversely clear positive associations with another trait related to the efficiency of feed utilization, i.e. residual feed intake (Nguyen et al., 2004; Gilbert et al., 2007; Cai et al., 2008). Growth rate has moderate negative, i.e. favorable, genetic associations with food conversion ratio (Clutter and Brascamp, 1998), indicating that the increased feed intake associated with a high daily gain is more than offset by the reduction in days on feed. Growth rate should, by construction, be independent from residual feed intake (RFI), but estimates may differ from zero due to correction of RFI for growth rate at the phenotypic and not at the genetic level (Kennedy et al., 1993), as well as to sampling error or inaccuracies of correlations used to compute RFI (Gilbert et al., 2007; Cai et al., 2008). Genetic associations between growth rate and feed efficiency during the fattening period with the same traits during early or adult life are poorly documented in the literature. Moderate positive genetic correlations between RFI of the growing pig and RFI or daily feed intake of the lactating sow are presented by Gilbert et al. (2010) at this meeting.

Association with carcass and meat quality traits

Dressing percentage has been shown to be genetically independent from growth rate in most pig populations (e.g. see review of Ducos, 1994). Its genetic association with feed intake is much less documented. Slightly negative r_g values (-0.20±0.06 and -0.11±0.11) were reported in French Large White and Landrace breeds, respectively, by Labroue et al. (1997). Similarly, a tendency towards a negative association with residual feed intake was reported by Gilbert et al. (2007).

Genetic correlations between growth rate during the fattening period and backfat thickness or carcass leanness are rather variable, with estimates ranging from favorable (-0.26 – Clutter and Brascamp, 1998) to rather strongly unfavorable (0.57 – Cai et al, 2008) values. Beyond sampling errors, this variability reflects significant breed differences, exemplified by the much stronger genetic antagonism between growth rate and carcass tissue composition observed in Piétrain as compared to Large White or Landrace breed in France (Ducos et al., 1993; Bidanel and Ducos, 1995). As outlined by Clutter and Brascamp (1998), such differences are likely to reflect variations in energy intake and its partitioning between lean and fat tissues. These variations also probably partly explain the substantial differences in genetic correlations between daily feed intake and backfat thickness (from 0.08 to 0.59 in the review of Clutter and Brascamp, 1998).

Genetic associations of growth rate with meat technological quality criteria, i.e. ultimate pH, color and water holding capacity, are close to zero in the majority of studies (De Vries et al., 1994; Hermesch et al., 2000a; Tribout and Bidanel, 2000), although both favorable (Hovenier et al., 1992; Lo et al., 1992) and unfavorable relationships (Van Wijk et al., 2005) have been reported in some cases. In a selection experiment for decreased muscle glycolytic potential, Larzul et al. (1999) did not find any significant correlative response in growth rate during the fattening period.

Genetic correlation estimates between feed intake and meat quality traits are less numerous. Null and slightly positive correlations between daily feed intake and a meat quality index combining ultimate pH, reflectance and water holding capacity were reported in French Large White and Landrace breeds, respectively, by Labroue et al. (1997). Hoque et al. (2009) found a strong positive correlation between daily feed intake (DFI) and pH at 45 min post mortem (0.66±0.19), but low and insignificant genetic correlations between DFI and ultimate pH, meat color and drip loss. Conversely, de Vries et al. (1994) reported moderate to strong associations between DFI and meat quality, in particular meat color, leading to an increased risk of dark, firm and dry meat with a higher feed intake.

It has to be emphasized that feed efficiency criteria consistently show some genetic antagonism (absolute values of r_g of the order of 0.20 to 0.40) with several meat quality traits, mainly meat color (Cameron et al., 1999; Hermesch et al., 2000a; Tribout and Bidanel, 2000), ultimate pH (Tribout and Bidanel, 2000), shear force value (Lonergan et al., 2001) and drip loss (Hermesch et al., 2000a). Similarly, significant genetic relationships of residual feed intake with meat color and ultimate pH have been reported by de Vries et al. (1994), Gilbert et al. (2007) and Hoque et al. (2009). Very strong correlative responses in meat quality traits to divergent selection for residual feed intake were also reported by Gilbert et al. (2007).

Estimates of r_g between growth rate and intramuscular fat content (IMF), a major determinant of meat sensory quality, do not show any consistent trend, with both negative (-0.09 - de Vries et al., 1994; -0.21±0.18 - Hermesch et al., 2000a) and positive (0.38±0.23 - Cai et al., 2008; 0.09±0.10 - Sellier et al., 2010) estimates. Moreover, Hermesch et al. (2000a), de Vries et al. (1994) and Cai et al. (2008) reported close to zero and positive genetic correlations between IMF and daily feed intake (0.03±0.17, 0.22 and 0.37±0.24, respectively).

Boar taint is another increasingly important quality issue in pig production due to the forthcoming regulations regarding castration of males. Genetic associations of boar taint or its major components, i.e. androstenone and skatole concentrations in the fatty tissue, with growth rate and feed intake have been investigated in divergent selection experiments for components of lean growth (Cameron et al., 2000) or for fat androstenone levels (Willeke and Pirchner, 1989; Sellier et al., 2000). A significantly positive correlative response in growth rate to selection for high androstenone level was obtained by Willeke and Pirchner (1989). Conversely, Sellier et al. (2000) reported low genetic correlations between fat androstenone level at 118 kg live weight and growth rate from 30 to 100 kg live weight.

Cameron et al. (2000) did not find any significant influence of selection for components of lean growth upon androstenone, skatole, indole levels or sensory panel scores of sex odours.

Association with reproductive traits

While genetic correlations between several male or female reproductive traits and growth rate have been thoroughly investigated, studies on associations with feed intake have so far been much less numerous. Both male and female sexual maturity traits tend to exhibit null or favorable genetic relationships with postweaning growth rate. In males, growth rate has been shown to have positive genetic correlations with testes measurements (Toelle et al., 1984; Young et al., 1986; Lubritz et al., 1991; Johnson et al., 1994) or testosterone levels (Lubritz et al., 1991) and to be weakly correlated with semen traits, i.e. volume, concentration, motility and percentage of abnormal spermatozoa (Wolf, 2009). Similarly, age at puberty of gilts shows negative, i.e. favorable, genetic relationships with growth rate (Hutchens et al., 1981; Rydhmer et al., 1992; Bidanel et al., 1996; Rosendo et al., 2007).

Former literature reviews (Brien, 1986; Haley et al., 1988) had concluded that litter size and weights are, on average, weakly correlated at the genetic level with growth rate during the fattening period. Yet, several recent publications have reported antagonistic relationships between sow prolificacy and growth (e.g. Ducos and Bidanel, 1996; Holm et al., 2004; Arango et al., 2005). This genetic antagonism could result from preferential resource allocation to growth in fast-growing animals at the expense of the ability of young sows to give birth to large litters (Rauw et al., 1999; Holm et al., 2004).

Significant negative genetic correlations also exist between litter size and preweaning weights or growth rate (e.g. Zhang et al., 2000). Bouquet et al. (2006) and Rosendo et al. (2007) recently showed that this antagonism is mainly due to a strong negative genetic correlation between maternal effects on piglet traits and direct effects on litter size. In contrast, correlations between direct effects on piglet growth and direct (sow) effects on prenatal survival or litter size appear to be low and non significant. As a consequence, selection for larger litter size tends to reduce piglet birth weight and preweaning growth rate through maternal effects. However, this decrease can be at least partly compensated by a positive response on direct effects because of a negative genetic correlation with maternal effects as well as, in many pig populations, by a favorable correlative response to selection for growth rate during the fattening period, as suggested by the favorable trend for piglet weight resulting from 21 years of selection in the French Large White breed (Tribout et al., 2003).

Available estimates of genetic correlations between feed intake during the growing period and litter size tend to show a weak association between the two traits. Short et al. (1994) and Hermesch et al. (2000b) found slightly negative correlations (-0.05 to -0.24), whereas weakly positive values (0.20 to 0.23) were reported by Crump et al. (1997). Yet, Kerr and Cameron (1995) reported differences in litter size of 1.9 and 0.9 piglets per litter at birth and at weaning, respectively, between lines selected for high and low daily feed intake of the growing animal. Although results are not directly comparable, it should be noted that Gilbert et al. (2010) also observed differences in litter size between 2 lines divergently selected for residual feed intake (RFI) during growth, but with a larger litter size in the line selected for low RFI. These results clearly show that feed intake / efficiency and litter size cannot be regarded as genetically independent traits.

Other traits

Leg weakness – due, in particular, to osteochondrosis – may be detrimental to animal welfare and has been shown to be associated with an increased risk of culling (e.g. Yazdi et al., 2000; Tarrés et al., 2006). Higher growth rate is often considered as being positively associated with increased leg weakness. Indeed, unfavorable genetic correlations between growth rate and osteochondrosis lesions have been reported in Danish Landrace and Yorkshire boars (Jorgensen and Andersen, 2000) and in Swiss pigs (Kadarmideen et al., 2004). More globally, a high growth rate has been shown to have antagonistic genetic associations with sow longevity (e.g. Lopez-Serrano et al., 2000). Relationships of feed intake during the fattening period and sow longevity are poorly documented. Conversely, feed intake of the lactating sow has been shown to be favorably associated with longevity at the phenotypic (e.g. Quiniou, 2003) and genetic (Hermesch, 2008) levels.

Resistance to heat stress or ability to have good performances under heat stress is also a challenge for the future, because the major part of the increase in world animal production should take place in the tropical area. Heat stress has well-known detrimental effects of growth rate and feed consumption of both growing pigs and breeding sows (Gourdine et al., 2006; Renaudeau et al., 2008). Zumbach et al. (2008a, b) investigated the effect of heat stress on growth and carcass traits. They found a higher heritability for growth under heat stress and proposed to quantify the effect of heat stress on pig performance using a heat load function.

Breeding for healthier pigs is a major target for the future. A potential approach is to select pigs for an increased immune response. Mallard et al. (1998) selected 2 lines of pigs for high or low immune response over 8 generations using an index combining antibody and cell-mediated response. They showed that pigs from the high immune response line have a higher growth rate, reaching market weight 10 days earlier than pigs from the low immune response line. Clapperton et al. (2006) showed difference in immune response between lines divergently selected for lean growth under restricted feeding, but did not show any difference between lines divergently selected for daily feed intake. More recently, Clapperton et al. (2008) showed significant genetic associations between growth rate and pig peripheral blood mononuclear subsets, and proposed to use the latter as immune trait markers.

Environmental concerns are also of major importance for the future. As emphasized by Kanis et al. (2005), the quantity of minerals and heavy metals excreted in manure per kilogram of meat produced largely depends on production and reproduction efficiencies. In particular, improving growth rate and feed intake would have a favorable environmental impact. Kanis et al. (2005) consequently suggest putting more emphasis on these traits in the aggregate breeding goal than the weight they have when based solely on their economic value.

Conclusion

This survey shows that daily weight gain and feed intake of the growing pig are genetically associated with many other traits of economic interest. Results about the associations with growth rate are rather well documented. Conversely, additional results are necessary to have a precise picture of the genetic relationships of feed intake in piglets, growing pigs and adult animals with other important traits. It should be emphasized that, here, we limited ourselves to a review of the classical parameters used in quantitative genetics. These genetic correlations may result from physiological relationships and from potential consequences of linked or pleiotropic QTL affecting correlated traits. We did not investigate this aspect of genetic associations between traits, since the knowledge on individual loci affecting traits of economic interest is still insufficient to have a precise picture of their real impact on genetic correlations. Although high throughput genomic technologies make it theoretically possible to precisely estimate the effects of each chromosomal region on traits of economic interest and to achieve a much better understanding of the genetic basis of relationships between traits, it clearly remains a formidable challenge for the forthcoming years.

References

Arango, J., Misztal, I., Tsuruta, S., Culbertson, M. and Herring, W. (2005) *J. Anim. Sci.* 83: 499-506.

Bidanel, J. P. and Ducos, A. (1995) *Journées Rech. Porcine en France* 27: 149-154.

Bidanel, J. P., Gruand, J. and Legault, C. (1996) *Genet. Sel. Evol.* 28: 103-115.

Bouquet, A., Ligonesche B., Canario, L. and Bidanel, J.P. (2006) *Journées Rech. Porcine* 38: 125-130.

Brien, F.D. (1986) *Anim. Breed. Abstr.* 54: 975-997.

Cai, W., Casey, D. S. and Dekkers, J. C. M. (2008) *J. Anim. Sci.* 86: 287-298.

Cameron, N. D., Curran, M. K. and Thompson, R. (1988) *Anim. Prod.* 46: 87-95.

Cameron, N. D., Nute, G. R., Brown, S. N., Enser, M. and Wood, J. D. (1999) *Anim. Sci.* 68: 115-127.

Cameron, N. D., Penman, J. C., Fisken, A. C., Nute, G. R., Perry, A.M. Whittington, F.W. (2000) *Meat Sci.* 54: 147-153.

Clapperton, M., Bishop, S. C. and Glass, E. J. (2006) *Anim. Sci.* 82: 867-876.

Clapperton, M., Glass, E. J. and Bishop, S. C. (2006) *Animal* 2: 1575-1584.

Clutter, A. C. and Brascamp, E. W. (1998) In: *The Genetics of the Pig,* CAB International, Oxon, UK, pp. 427-462.

Crump, R. E., Thompson, R., Haley, C. S. and Mercer, J. (1997) *Anim. Sci.* 65: 291-298.

de Vries, A. G., van der Wal, P. G., Long, T., Eikelenboom, G. and Merks, J. W. M. (1994) *Livest. Prod. Sci.* 40: 277-289.

Ducos, A. (1994) *PhD Thesis,* Institut National Agronomique Paris-Grignon, France, 222 p.

Ducos, A. and Bidanel, J. P. (1996) *J. Anim. Breed. Genet.* 113: 493-504.

Ducos, A., Bidanel, J. P., Boichard, D. and Ducrocq, V. (1993) *Genet. Sel. Evol.* 25: 475-493.

Gilbert, H., Bidanel, J. P., Gruand, J., Caritez, J. C., Billon, Y., Guillouet, P., Lagant, H., Noblet, J. and Sellier, P. (2007) *J. Anim. Sci.* 85: 3182-3188.

Gilbert, H., Billon, Y., Lagant, H., Calderon, J. A., Guillouet, P., Bidanel, J. P., Noblet, J. and Sellier, P. (2010) In: *Proc. 9th WCGALP* (in press).

Gourdine, J. L., Renaudeau, D., Bidanel, J. P. and Noblet, J. (2006) *J. Anim. Sci.* 84: 469-480.

Haley, C. S., Avalos, E. and Smith, C. (1988) *Anim. Breed. Abstr.* 56: 317-332.

Hermesch, S., Luxford, B. G. and Graser, H. U. (2000a) *Livest. Prod. Sci.* 65: 249-259.

Hermesch, S., Luxford, B. G. and Graser, H. U. (2000b) *Livest. Prod. Sci.* 65: 261-270.

Hermesch, S., Jones, R. and Bunter, K.L. (2008) AGBU Pig Genetics Workshop notes, pp 55-66.

Holm, B., Bakken, M., Klemtsdal, G. and Vangen, O. (2004) *J. Anim. Sci.* 82: 3458-3464.

Hoque, M. A., Katoh, K. and Suzuki, K. (2009) *J. Anim. Sci.* 87: 3069-3075.

Hovenier, R., Kanis, E., Van Asseldonk, T. and Westerink, N. G. (1992) *Livest. Prod. Sci.* 32: 309-321.

Hutchens, L. K., Hintz, R. L. and Johnson, R. K. (1981) *J. Anim. Sci.* 53: 946-951.

Johnson, R. K., Eckardt, G. R., Rathje, T. A. and Drudik, D. K. (1994) *J. Anim. Sci.* 72: 1978-1988.

Jorgensen, B. and Andersen, S. (2000) *Anim. Sci.* 71: 427-434.

Kadarmideen, H. N., Schwörer, D., Ilahi, H., Malek, M. and Hofer, A. (2004) *J. Anim. Sci.* 82: 3118-3127.

Kanis, E., De Greef, K. H., Hiemstra, A. and van Arendonk J. A. M. (2005) *J. Anim. Sci.* 83: 948-957.

Kennedy, B.W., Van der Werf, J.H.J., Meuwissen, T.H.E. (1993) *J. Anim. Sci*. 71: 3239-3250.

Kerr, J. C., and Cameron, N. D. (1995) *Anim. Sci.* 60: 281-290.

Labroue, F. 1995. *INRA Prod. Anim.* 8: 239-250.

Labroue, F., Guéblez, R. and Sellier, P. (1997) *Genet. Sel. Evol.* 29: 451-468.

Larzul, C., Le Roy, P., Gogué, J., Talmant, A., Monin, G. and Sellier, P. (1999) *Genet. Sel. Evol.* 31: 149-161.

Lo, L. L., McLaren, D. G. , McKeith, F. K., Fernando, R. L. and Novakofski, J. (1992) *J. Anim. Sci.* 70: 2387-2396.

Lonergan, S. M., Huff-Lonergan, E., Rowe, L. J., Kuhlers, D. L. and Jungst, S. B. (2001) *J. Anim. Sci.* 79: 2075-2085.

Lopez-Serrano, M., Reinsch, N., Looft, C. and Kalm, E. (2000) *Livest. Prod. Sci.* 64: 121-123.

Lubritz, D., Johnson, B. and Robison, W. O. (1991) *J. Anim. Sci.* 69: 3220-3224.

Mallard, B. A., Wilkie, B. N., Kennedy, B. W., Gibson, J. and Quinton, M. (1998) In: *Proc. 6th WCGALP* 27: 257-264.

McPhee, C. P., Brennan, P. J. and Duncalfe F. (1979) *Anim. Prod.* 28: 79-85.

Nguyen Hong, N., McPhee, C. P. and Wade C. M. (2004) *Pig News and Information* 25: 149N-163N.

Quiniou, N. (2003) *Techni-Porc* 26: 19-27.

Rauw, W. M., Luiting, P., Beilharz, R. G., Verstegen, W. M. A. and Vangen, O. (1999) *Livest. Prod. Sci.* 60: 329-342.

Renaudeau, D., Kerdoncuff, M., Anais, C. and Gourdine, J. L. (2008) *Animal* 2: 1619-1626.

Roehe, R. (1999) *J. Anim. Sci.* 77: 330-343.

Rosendo, A., Canario, L., Druet, T., Gogué, J. and Bidanel, J. P. (2007) *J. Anim. Sci.* 85: 3209-3217.

Rydhmer, L. Johansson, K., Stern, S. and Eliasson-Selling, L. (1992) *Acta Agric. Scand.* 42: 211-219.

Sellier, P., Le Roy, P., Fouilloux, M. N., Gruand, J. and Bonneau, M. (2000) *Livest. Prod. Sci.* 63: 265-274.

Sellier, P., Maignel, L. and Bidanel, J. P. (2010) *Animal* 4: 497-504.

Short, T. H., Wilson, E. R. and McLaren, D. G. (1994) In: *Proc. 5th WCGALP, vol.17*: 413-416.

Solanes, F. X. Grandinson, K., Rydhmer, L., Stern, S., Andersson, K. and Lundeheim, N. (2004) *Livest. Prod. Sci.* 88: 199-212.

Tarrés, J., Bidanel, J. P., Hofer, A. and Ducrocq, V. (2006) *J. Anim. Sci.* 84: 2914-2924.

Toelle, V. D., Johnson, B. H. and Robison, O. W. (1984) *J. Anim. Sci.* 59: 967-973.

Tribout, T., and Bidanel J. P. (2000) In: *E. A. A. P. Publication No. 100,* Wageningen Pers, Wageningen, The Netherlands, pp. 37-41.

Tribout, T., Caritez, J. C., Gogué, J., Gruand, J., Billon, Y., Bouffaud, M., Lagant, H., Le Dividich, J., Thomas, F., Quesnel, H., Guéblez, R. and Bidanel, J P. (2003) *Journées Rech. Porcine* 35: 285-292.

Van Wijk, H. J., Arts, D. J. G., Matthews, J. O., Webster, M., Ducro, B. J. and Knol, E. F. (2005) *J. Anim. Sci.* 83: 324-333.

von Felde, A., Roehe, R. and Kalm, E. (1996) *Züchtungskunde* 68: 305-318.

Whittemore, C. T. (1994) *Outlook on Agriculture* 23: 55-59.

Willeke, H. and Pirchner, F. (1989) *J. Anim. Breed. Genet.* 106: 312-317.

Wolf, J. (2009) *Animal* 3: 1094-1099.

Yazdi, M. H., Rydhmer, L., Ringmar-Cederberg, E., Lundeheim, N. and Johansson, K. (2000) *J. Anim. Sci.* 71: 1-9.

Young, L. D., Leymaster, K. A. and Lundstra, D. D. (1986) *J. Anim. Sci.* 63: 17-26.

Zhang, S., Bidanel, J. P., Burlot, T., Legault, C. and Naveau, J. (2000) *Genet. Sel. Evol.* 32: 41-56.

Zumbach, B., Misztal, I., Tsuruta, S., Sanchez, J. P., Azain, M., Herring, W., Holl, J., Long, T. and Culbertson, M. (2008a) *J. Anim. Sci.* 86: 2076-2081.

Zumbach, B., Misztal, I., Tsuruta, S., Sanchez, J. P., Azain, M., Herring, W., Holl, J., Long, T. and Culbertson, M. (2008b) *J. Anim. Sci.* 86: 2082-2088.