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Environmental responsiveness of fibre diameter in grazing fine wool Merino sheep

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Abstract. Fibre diameter, fibre length, and the ratio of fibre length growth to mean fibre diameter (L/D), fibre diameter profile characteristics, and staple strength were examined in 16 fine wool Merino wethers in a 12-month field experiment. Variations in fibre diameter, fibre length, and L/D were shown to be associated with fibre diameter profile characteristics and staple strength. At constant fibre diameter, L/D was significantly positively related to variation in fibre diameter along the staple. A positive correlation between seasonal variation in L/D and variation in diameter between fibres was also observed. Staple length was significantly positively correlated with along-staple variation in fibre diameter and negatively correlated with variation in fibre diameter among fibres. Among-fibre variation in fibre diameter was not significantly correlated with along-staple variation in fibre diameter. Seasonal variation in fibre length growth, fibre diameter, and the ratio of length to diameter throughout the year was associated with increased variation in fibre diameter along the fibre diameter profile and reduced staple strength in grazing sheep. Seasonal variation in fibre diameter was mostly related to mean fibre diameter, L/D, and seasonal variation in fibre length growth rate. Changes in fibre diameter throughout the year were also related to seasonal changes in body weight, fat depth, and skin thickness.

Additional keywords: fibre diameter profile, L/D, body weight, fat depth, skin thickness.

Introduction

Fibre diameter profile (FDP) characteristics vary among environments, bloodlines, sire groups, and individual sheep (Jackson and Downes 1979; Denney 1990; Hansford 1994, Adams *et al.* 1996, 1997, 1998; Adams and Briegel 1998; Brown *et al.* 1999, 2002) and explain significant variation in staple strength (Adams and Briegel 1998; Adams *et al.* 1998; Peterson *et al.* 1998; Brown *et al.* 1999, 2002). At present, variation among sheep and bloodlines in their seasonal changes in fibre diameter is not fully understood.

The contribution of fibre diameter and length to wool growth varies among fibres, over time, and between sheep. The ratio of fibre length growth to fibre diameter (L/D) is an important consideration for changing wool growth and the characteristics of the fibre grown and also may determine the way in which it responds, in terms of fibre diameter, to changes in nutrition (Woods and Orwin 1988; Hynd 1992). Although individual sheep maintain a relatively constant L/D, there are significant differences among fibres and sheep in L/D (Woods and Orwin 1988), ranging approximately from 10 : 1 to 30 : 1 (Hynd 1992; Reis 1992). Therefore direct or indirect selection of sheep with high L/D should have 2 desirable outcomes: greater fibre lengths and reduced fibre diameter variability along fibres (Hynd 1992). Actual changes in fibre length and fibre diameter are also highly variable between sheep (Hynd 1992). The ratio of the change in fibre length to the change in fibre diameter for individual sheep ranged from 13 : 1 to 80 : 1 (Hynd 1992). Differences in these characteristics may explain some of the large differences among sheep in staple strength.

L/D was thought to be independent of nutrition (Downes 1971; Cottle 1987; Reis 1992) and remain constant with changes in the rate of wool growth (Reis 1991). Studies conducted throughout a year of wool growth demonstrated that L/D exhibits a seasonal trend (Woods and Orwin 1988; Schlink *et al.* 1996*a*). No explanation is apparent for these trends; however, it has been suggested that the mechanisms determining these growth parameters in the follicle are complex (Woods and Orwin 1988). The evidence indicates that not only does the L/D vary among sheep but the level of seasonal variation of these characteristics also varies among sheep (Woods and Orwin 1988). Variation

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among sheep in the levels of seasonal variation in fibre length growth rate, fibre diameter, and L/D may influence staple strength.

L/D may influence the degree to which individual sheep respond to their environment and differences in L/D may be associated with differences in FDP characteristics and staple strength; however, these relationships have not yet been investigated.

Sheep with a lower initial fibre diameter can show a smaller relative proportion of fibre diameter change with improved nutrition compared with those sheep with a higher initial fibre diameter (Jackson and Downes 1979; Thompson 1993; Bow and Hansford 1994; Earl *et al.* 1994; Kopke and Hocking Edwards 1998; Brown *et al.* 2002). Therefore, differences among sheep in FDP characteristics may be influenced by differences in mean fibre diameter. These relationships have not been investigated in combination with L/D, staple strength, and body traits.

Wool growth is influenced by many physiological and nutritional factors throughout the year that vary throughout the year (Adams *et al.* 1994). The major factor controlling wool growth is the availability of nutrients to the wool follicle (Allden 1979; Reis 1979, 1991). The supply of these nutrients is influenced by changes in nutrient partitioning and body composition. Given that it is the skin that supports and nourishes the massive population of wool follicles it is not surprising that skin thickness is related to wool growth (Gregory 1982; Williams and Thornberry 1992) and is related to the body condition of sheep (Hutchinson 1957; Lyne 1964; Williams and Morley 1994; Murray 1996; Schlink *et al.* 1996*b*). It may be possible that differences in skin thickness and seasonal variation in skin thickness among animals may be associated with differences in FDPs. Sheep that have less variation in skin thickness throughout the year may be able to better maintain skin condition and therefore follicle nutrition. This would result in reduced fibre diameter variation along the FDP.

Adams and Briegel (1998) suggested that large body size might provide a buffer of body reserves for wool growth. Furthermore, empty body weight, carcass fat, carcass muscle, and visceral lean can show significant oscillation throughout the year when sheep are fed a constant intake (Ball *et al.* 1996). This may be due to seasonal shifts in metabolism and seasonal effects on the priorities for tissue deposition and retrieval that are independent of variation in feed intake and seasonal variation in the utilisation of feed. Differences among sheep in body weight and composition, and seasonal variation in these traits, may be associated with seasonal variation in fibre diameter and staple strength.

This study aims to define the relationships between initial fibre diameter, average L/D, and seasonal variation in L/D and FDP variation and staple strength. The influence of seasonal changes in body weight, body condition, and skin thickness on these relationships will also be investigated.

Materials and methods

Animals

Forty-eight 2-year-old fine wool Merino wethers were obtained from the Kirby Rural Research Station. All animals originated from the same mob and had similar management histories. The mean fibre diameter of the 48 wethers was measured using a small wool sample from the left-hand mid-side patch. This sample was scoured (3 hexane washes followed by 1 hot water wash), dried, and the fibre diameter was measured using the Sirolan Laserscan (Sirolan Laserscan Technology) (Charlton 1995). The 48 animals were ranked on mean fibre diameter and divided into 16 consecutive groups of 3 animals. Sixteen experimental animals were then selected using a stratified selection technique. One sheep was randomly selected from each group to give a relatively even distribution of initial fibre diameters (IMFD).

After the animals were selected, all the sheep were maintained as a single grazing mob (in an experimental paddock) for a 4-week pre-experimental period to reduce the environmental differences among sheep in fibre diameter.

Environment

The sheep were maintained for the duration of the experiment at the Kirby Rural Research Station, 10 km north-west of Armidale, NSW (30°31′00 S, 151°39′50 E). The experimental paddocks consisted of native and improved grass pasture species.

Sampling regime

The animals were sampled at 12 times throughout the experiment, approximately 4 weeks apart. At each of these samplings the unfasted body weight (Bwt) of the sheep was measured using electronic sheep scales (Ruddweigh). The skin thickness and fat depth were measured (using callipers and ultrasound) and a dyeband inserted at each of these samplings as described below.

Wool measurements

Dyebands

At each sampling time a dyeband was inserted at the base of a line of staples (approx. 10-cm long running in a dorsal–ventral direction) using a blunt 21-gauge needle and 1-mL syringe. The dyeband fluid was mixed at 0.8% (w/v) Durafur Black flakes and 0.8% (w/v) concentrated hydrogen peroxide dissolved in cold water. These staples were located approximately 10 cm anterior of the right mid-side patch.

At the end of the experiment a mid-side sample was collected. This sample was not from the true mid-side region as this site was used for skin measurements. The sample used to represent the mid-side sample was collected adjacent to the mid-side area. This sample consisted of all wool staples between the clipped patch used for the skin thickness measurements and the staples that were dyebanded.

Three wool staples were randomly selected from the dyebanded staples and used to measure fibre diameter at, and staple length between, each dyeband. Staple length was measured 3 times between each dyeband using a standard steel ruler. These measurements were averaged to give staple length growth between each dyeband. From these measurements, average ($AvSL_{Bands}$) and variation ($SDSL_{Bands}$ and $CVSL_{Bands}$) in staple length growth between the dyebands were calculated. A 2-mm snippet was guillotined at each dyeband on each of the 3 staples, washed (3 × 5-min hexane washes and one 5-min hot water wash), dried overnight, and the fibre diameter measured using 500 counts by the Sirolan Laserscan.

L/Ds

Fibre length and fibre diameter were measured between Days 64–92, 204–232, and 318–344 using autoradiography (modified from Hynd 1994). The measurements were made on a small bundle of staples located approximately 120 mm dorsally of the right mid-side patch. Each measurement period consisted of 2 intradermal injections approximately 28 days apart with 0.3 mL of normal saline solution containing 5.1 µCi/mL of ^{35}S-cysteine hydrochloride (based on activity at harvest). Twenty-one days after the second injection the labelled staples were harvested (clippers), cleaned (3 hexane washes followed by 1 hot water wash), stained with picric acid, washed in hot water, and dried overnight. Approximately 70 fibres were randomly selected from the sample and mounted on glass slides with Polyvinylpyrrolidone (BDH Limited Poole England) and exposed to X-ray film (AGFA Structurix D7FW) for 7 days. The film was superimposed onto the slides with DPX (Ajax Chemicals). The fibre diameter was measured at 10 sites approximately equidistant between the labelled areas on at least 50 fibres, using an image analysis system (Leica Quantimet 500MC Leica Cambridge Ltd). The image analysis program was calibrated using a standard haemocytometer. Fibre length was measured on 50 fibres for each sheep by tracing the fibre between the labelled points using the same image analysis system. The mean fibre diameter, fibre diameter variation, mean fibre length, and fibre length variation for the period of wool growth were calculated for each sheep. The ratio of fibre length growth per day (µm/day) to mean fibre diameter was calculated (L/D). The 3 periods were combined to obtain average fibre length (AvFL), fibre length variation (AvFLCV), L/D (AvL/D), variation in L/D (L/DCV), variation in average fibre diameter (FDCV), and the variation in fibre growth rate (FGCV) for each animal. The average absolute change in fibre length growth rate (△FL), fibre diameter (△FD), and the ratio of change in fibre length growth to change in fibre diameter (△FL/△FD) between the 3 measurement periods were also calculated.

FDPs and FDP characteristics

A FDP was generated for each sheep using the FDP prediction technique (1 in 4 level of inclusion) described by Brown *et al*. (2000). Briefly, a wool staple was randomly selected from the mid-side sample of each animal and was scoured (3 × 5 min in hexane and 1 × 5 min in hot water), dried overnight, wrapped in cling wrap, and segmented in a series of 2-mm snippets for the entire length of the staple. The total number of snippets in the original FDP was recorded. The first, last, and every fourth snippet in-between were measured for fibre diameter using the Sirolan Laserscan. A cubic spline was fitted using S-Plus (Statistical Sciences 1995), which generated a predicted FDP for each animal, the same length as the original FDP.

The FDP for each sheep was described using a number of characteristics, which were selected to suit the general shape of the FDP, which was a generalised ‘N shape’. Three major points were identified in each of the profiles at which fibre diameter and position were recorded. These points were at the position of the minimum fibre diameter (Mindiam) between the 2 distinct points of maximum fibre diameter, the maximum fibre diameter between the Mindiam and the tip of the profile, and the maximum fibre diameter between the Mindiam and the base of the profile. Using these 3 points, 2 rates of fibre diameter change were calculated. The first rate of change was calculated between the first point of maximum fibre diameter and the Mindiam (Roc1) and the second rate of change was calculated between the Mindiam and the second point of maximum fibre diameter (Roc2). These rates of change were calculated by fitting a linear regression to all points between the respective maximum and minimum. The FDP characteristics of overall maximum fibre diameter (Max) and along-staple variation in fibre diameter (AstCV) were also calculated for each FDP. The coefficient of variation of fibre diameter within each snippet was averaged over all snippets within each original FDP to give an estimate of between-fibre variation in fibre diameter (AvSnipCV).

Staple strength and staple length

Ten staples were randomly selected from the mid-side sample by using a sampling board. The board was 24-cm wide and 30-cm long, with 5 randomly placed holes (32 mm in diameter). This board was randomly placed on the mid-side sample, which was spread out on a bench. A staple was randomly selected from each hole and the board was rotated 90 degrees and another staple selected from each hole. These staples were left to condition overnight (20 ± 2°C and 63 ± 2% humidity). Staple length (SL) and staple strength (SS) were measured for each staple using the Agritest StapleBreaker Model 2 (Vizard *et al*. 1994; Baxter 1996).

Fibre diameter

The remaining mid-side sample was used to measure mean fibre diameter. The entire sample of approximately 10 g was scoured using 2 hot water and Lissapol detergent (manufactured by ICI Chemical and distributed by Spectrum Distributors as Hydropol TN450) washes and a final plain hot water wash. The samples were then spun for approximately 2 min and dried at 70°C for 30 min. The sample was then mini-cored and the fibre diameter (mid-side MFD) and fibre diameter variation (mid-side MFDCV) measured using 2000 counts by the Sirolan Laserscan.

Fat depth

The depth of subcutaneous fat at the C site (over the eye muscle of the 12th rib) was measured within 3 days either side of each of the 12 sampling times. These measurements were made using an Aloka 500V real time ultrasound scanner at a frequency of 3.5 Mega Hertz. The probe was 17.5-cm long and designed for use in cattle. Although it would have been more appropriate to use a smaller, higher frequency probe, financial constraints made this unfeasible.

Skin thickness

The average skin thickness of the sheep was measured at each sampling time using a technique described by Williams and Thornberry (1992). Skin thickness was measured at 2 points randomly selected on the right mid-side after close clipping (Oster small animal clippers, size 30 blade). These 2 points were marked with a permanent marking pen and used for the skin measurements at each sampling. A double fold of skin was measured using dial gauge callipers that exerted a constant pressure of 1250 g/cm^2 (Lyne 1964). A measurement was made at each spot with the callipers facing in anterior–posterior direction and a second measurement was made in a dorsal–ventral direction. For each animal, average skin thickness (Skin) and variation in skin thickness (SkinCV) over the experimental period were calculated.

Statistical analysis

The strength and direction of the relationships between the various fibre, staple, and body characteristics were examined using simple correlation and stepwise multiple regression analysis performed using the CORR and REG procedures of SAS (1990). The stepwise multiple regression fitted the most highly correlated variable first and then individual variables were added one at a time to see which had the greatest effect on the proportion of variation explained. Only variables that added significantly ($P < 0.15$) to the explained variance were retained in the model. Least squares analysis of variance was also used to compare L/D among measurements and initial and mid-side mean fibre diameter measurements. The model for each analysis of variance included the random effects of animal and measurement within animal.

Results

There was large variation (>20% CV) among the 16 experimental sheep for most traits and also in their FDP. FDPs from sheep with similar initial mean fibre diameter and FDP length exhibited markedly different patterns of fibre diameter throughout the experiment (Fig. 1). Body weight (Bwt) showed a steady increasing trend throughout the experiment, rising from 40.1 kg at the start of the experiment to 51.1 kg at the end of the experiment (Fig. 2). Fat depth showed a seasonal trend that was similar to that of the FDPs and feed on offer. The variation in skin thickness throughout the experiment was smaller relative to that of Fat and the FDPs.

There were significant ($P < 0.001$) differences in L/D among animals and among measurements of L/D. The first L/D measurement was significantly lower ($P < 0.05$) than the 2nd and 3rd measurements (the least square means were 16.8 ± 0.3, 18.4 ± 0.3, and 18.9 ± 0.3 μm/day.μm for the 1st, 2nd, and 3rd measurements, respectively) but highly correlated with each ($r = 0.87$, $P < 0.05$ and $c = 0.93$, $P < 0.05$, respectively). The 2nd and 3rd L/D measurements were also highly correlated ($r = 0.90$, $P < 0.05$) and not significantly different ($P > 0.05$).

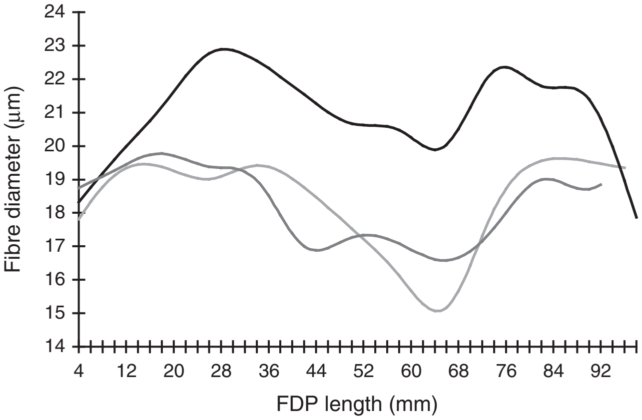

Fig. 1. Example of the FDPs from 3 of the experimental animals of similar fibre diameter profile length and initial fibre diameter.

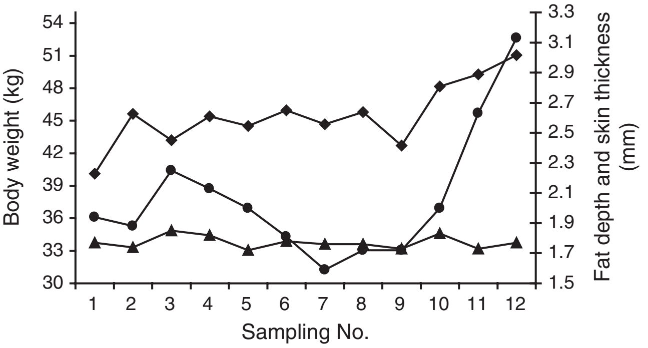

Fig. 2. Body weight (◆), fat depth (●) and skin thickness (▲) throughout the experimental period.

Relationship between the FDP characteristics and the fibre-based measurements

Average L/D was negatively correlated with Max, Mindiam, Roc1, and Roc2 (Table 1). Over all animals in the study, average L/D was not highly correlated with AstCV ($r = 0.14$); however, there were strong relationships observed within fibre diameter groups. The relationship between average L/D and AstCV increased to $r = 0.70$ when only the 8 animals with mid-side MFD values between 17.5 and 18.8 μm were examined. This relationship further strengthened ($r = 0.98$) when the 5 animals with values 18.2 and 18.8 μm were compared.

Seasonal variation in L/D (L/DCV) was negatively correlated with along-staple variation in fibre diameter ($r = -0.36$) and the rates of fibre diameter change but positively correlated with variation among fibres ($r = 0.46$). Average fibre length growth was positively correlated with along-staple variation in fibre diameter ($r = 0.52$). ΔFL and ΔFD were positively correlated with all FDP characteristics. In a multiple regression equation the characteristics of CVSL (bands) (13.6%), ΔFD (42.3%), ΔFL (2.5%), and FDCV (18.6%) explained in total 77% ($P < 0.05$) of the variation of AstCV. The remaining characteristics did not significantly explain any additional variation in AstCV.

Relationship between FDP characteristics and mid-side wool quality characteristics

Initial MFD and mid-side MFD were significantly and positively correlated with all FDP characteristics except AvSnipCV (Table 2). Initial MFD and AstCV were positively associated ($r = 0.61$). Initial MFDCV was only significantly correlated with AvSnipCV ($r = 0.53$), whereas mid-side fibre diameter variation was significantly and positively correlated with absolute fibre diameter values in the FDP. Mid-side variation in fibre diameter was not significantly correlated with along-staple variation in fibre diameter ($r = -0.09$, $P > 0.05$) but significantly positively correlated with between-fibre variation in fibre diameter ($r = 0.79$, $P < 0.001$).

Staple length was significantly positively correlated with along-staple variation in fibre diameter but negatively correlated with variation in fibre diameter among fibres. Among fibre variation in fibre diameter was also not significantly correlated with along-staple variation in fibre diameter ($r = -0.10$, $P > 0.05$).

Relationship between FDP characteristics and body traits

Variation in body weight (BwtCV) was significantly positively correlated with AstCV. Skin thickness was positively correlated with absolute fibre diameter within the

Table 1. Correlation coefficients for the relationships between the wool fibre characteristics and the fibre diameter profile characteristics

Max, maximum fibre diameter; Mindiam, minimum fibre diameter; AstCV, coefficient of variation in fibre diameter along the fibre diameter profile; Roc1, first rate of fibre diameter change; Roc2, second rate of fibre diameter change; AvSnipCV, average along the fibre diameter profile of the CV in fibre diameter within each snippet; AvL/D, average ratio of fibre length to fibre diameter over the three measurement periods; L/DCV, CV in the ratio of fibre length to fibre diameter over the three measurement periods; FGCV, variation in FG between the 3 measurement periods; FDCV, CV in FG between the 3 measurement periods; AvFL, average fibre length; AvFLCV, average CV in fibre length over the 3 measurement periods; △FL, change in fibre length growth between measurements; △FD, change in fibre diameter between measurements; AvSL(bands), the average staple length growth between dyebands; CVSL(bands), CV in staple length growth between dyebands

Characteristics	Max	Mindiam	AstCV	Roc1	Roc2	AvSnipCV
AvL/D	−0.61*	−0.70*	0.14	−0.42*	−0.08	0.12
L/DCV	0.16	0.28	−0.36	−0.17	−0.19	0.46*
FGCV	−0.08	−0.20	0.32	0.09	0.04	−0.17
FDCV	−0.11	−0.09	0.11	0.42*	−0.16	0.10
AvFL	−0.08	−0.25	0.52*	−0.11	0.31	0.17
AvFLCV	0.35	0.48*	−0.27	−0.10	−0.37	−0.15
△FL	0.05	0.10	0.46*	0.15	0.12	−0.12
△FD	0.43*	0.32	0.65*	0.74*	0.44*	−0.18
△FL/△FD	0.00	−0.14	0.29	−0.04	−0.02	−0.31
AvSL(bands)	0.28	0.06	0.63*	0.09	0.50*	0.23
CVSL(bands)	0.18	0.03	0.18	−0.01	−0.13	0.33

*$P < 0.05$.

Table 2. Correlation coefficients for the relationships between the wool quality characteristics and the fibre diameter profile characteristics

Max, maximum fibre diameter; Mindiam, minimum fibre diameter; AstCV, CV in fibre diameter along the fibre diameter profile; Roc1, first rate of fibre diameter change; Roc2, second rate of fibre diameter change; AvSnipCV, average along the fibre diameter profile of the CV in fibre diameter within each snippet; IMFD, initial mean fibre diameter (at start of experiment); IMFDCV, CV in fibre diameter from measurement of initial mean fibre diameter; Mid-side MFD, mean fibre diameter measurement from mid-side sample at the end of experiment; Mid-side MFDCV, CV in fibre diameter from measurement of mid-side mean fibre diameter; SL, staple length

Characteristics	Max	Mindiam	AstCV	Roc1	Roc2	AvSnipCV
IMFD	0.86*	0.79*	0.61*	0.61*	0.59*	0.22
IMFDCV	0.20	−0.06	0.30	0.01	0.21	0.53*
Mid-side MFD	0.92*	0.88*	0.45*	0.51*	0.44*	0.42
Mid-side MFDCV	0.54*	0.63*	−0.09	0.03	−0.09	0.79*
SL	−0.05	−0.19	0.51*	0.01	0.50*	−0.54*

*$P < 0.05$.

FDP and variation among fibres but negatively correlated with variation in fibre diameter along fibres and the rates of fibre diameter change (Table 3). Seasonal variation in skin thickness and fat depth was generally positively correlated with all FDP characteristics.

Average fat depth was negatively correlated with all FDP characteristics except AvSnipCV, and seasonal variation in fat depth was negatively correlated with variation in fibre diameter among fibres ($r = -0.46$).

Body weight was negatively correlated with skin thickness ($r = -0.23$) and positively correlated with fat depth ($r = 0.62$). Seasonal variation in body weight was not significantly ($P > 0.05$) but positively correlated with both seasonal variation in skin thickness and fat depth ($r = 0.22$ and 0.14) and seasonal variation in skin thickness was not correlated ($r = 0.07$) with seasonal variation in subcutaneous fat.

Multiple regression analysis indicated that seasonal variation in skin thickness (21.9%) and average skin thickness (14.2%) were the only body traits that significantly explained the variation in along-staple fibre diameter ($r^2 = 0.36, P < 0.05$).

Table 3. Correlation coefficients for the relationships between the body characteristics and the fibre diameter profile characteristics

Max, maximum fibre diameter; Mindiam, minimum fibre diameter; AstCV, CV in fibre diameter along the fibre diameter profile; Roc1, first rate of fibre diameter change; Roc2, second rate of fibre diameter change; AvSnipCV, average along the fibre diameter profile of the CV in fibre diameter within each snippet; Bwt, average body weight; BwtCV, CV in body weight throughout experiment; Skin, average skin thickness; SkinCV, CV in skin thickness throughout experiment; Fat, average subcutaneous fat depth; BwtCV, CV in subcutaneous fat depth throughout experiment

Characteristics	Max	Mindiam	AstCV	Roc1	Roc2	AvSnipCV
Bwt	−0.11	−0.02	−0.02	−0.40	−0.24	0.11
BwtCV	0.30	0.24	0.46*	0.36	0.37	−0.10
Skin	0.35	0.48*	−0.46*	−0.10	−0.27	0.61*
SkinCV	0.20	0.03	0.47*	0.56*	0.43*	0.31
Fat	−0.30	−0.14	−0.11	−0.45*	−0.26	0.14
FatCV	0.01	0.04	0.09	0.35	0.57*	−0.46

*$P < 0.05$.

Relationships between the fibre-based and mid-side measurements

Initial MFD was positively correlated with ΔFL, ΔFD, and ΔFL/ΔFD ($r = 0.31$, 0.63, and 0.17, respectively). Average L/D was positively correlated with ΔFL and the ratio of ΔFL/ΔFD ($r = 0.67$ and 0.41 respectively) while negatively correlated with ΔFD ($r = -0.12$). ΔFL was positively correlated with ΔFD ($r = 0.35$). Sheep that had higher average L/D also had less seasonal variation in L/D ($r = -0.47$), mid-side mean fibre diameter ($r = -0.65$) and mid-side fibre diameter variation ($r = -0.61$). Mid-side fibre diameter variation was also significantly positively correlated ($r = 0.62$) with variation in fibre length.

Relationships between the fibre-based measurements and body traits

Body weight ($r = 0.30$ and 0.33) and fat depth ($r = 0.50$ and 0.53) were both positively correlated with L/D and fibre length growth, whereas average skin thickness was negatively correlated with L/D and fibre length growth ($r = -0.75$ and -0.71). Seasonal variation in body weight, fat depth, and skin thickness was positively correlated with the absolute changes in fibre length and diameter among the measurements of L/D.

Relationship between FDP and mid-side measurements with staple strength

AvSnipCV, initial MFDCV, mid-side MFD, and mid-side MFDCV were all significantly negatively correlated with staple strength (Table 4). In a multiple regression of FDP characteristics with staple strength, AvSnipCV significantly explained 50.6% of the variation in staple strength ($P < 0.05$), whereas the remaining FDP characteristics did not significantly explain any additional variation in staple strength. Mid-side fibre diameter variation (MFDCV) was the only mid-side wool quality characteristic that significantly explained any proportion (36%) of the variation of staple strength ($P < 0.05$). In the stepwise multiple regression with all FDP and mid-side wool quality characteristics, AvSnipCV (50.6%) and staple length (8.4%) significantly explained 59% ($P < 0.05$) of the variation in staple strength.

Table 4. Correlation coefficients for the relationships between the fibre diameter profile and mid-side measurements and staple strength

Max, maximum fibre diameter; Mindiam, minimum fibre diameter; AstCV, CV in fibre diameter along the fibre diameter profile; Roc1, first rate of fibre diameter change; Roc2, second rate of fibre diameter change; AvSnipCV, average along the fibre diameter profile of the CV in fibre diameter within each snippet; IMFD, initial mean fibre diameter (at start of experiment); IMFDCV, CV in fibre diameter from measurement of initial mean fibre diameter; Mid-side MFD, mean fibre diameter measurement from mid-side sample at the end of experiment; Mid-side MFDCV, CV in fibre diameter from measurement of mid-side mean fibre diameter; SL, staple length

Characteristics	Max	Mindiam	AstCV	Roc1	Roc2	AvSnipCV
Correlation	−0.22	−0.06	−0.17	0.13	0.08	−0.71*
Characteristics	IMFD	IMFDCV	Mid-side MFD	Mid-side MFDCV	SL	
Correlation	−0.16	−0.66*	−0.24	−0.60*	0.14	

*$P < 0.05$.

Relationship between the fibre-based measurements and staple strength

All the characteristics except △FD and FDCV were negatively correlated with staple strength (Table 5). Average L/D was not significantly correlated with staple strength. Seasonal variation in fibre length growth was negatively correlated with staple strength, $r = -0.23, -0.31$, and -0.63 for FGCV, △FL, and $\text{CVSL}_{\text{Bands}}$, respectively. The ratio of △FL to △FD and FLCV were also significantly negatively correlated with staple length ($r = -0.51$ and -0.47).

When combined in a stepwise multiple regression the only characteristics from Table 5 that significantly explained variation in staple strength were $\text{CVSL}_{\text{Bands}}$ (39.9%), L/DCV (10.9%), and △FL/△FD (16.9%), which in total explained 67.7% ($r^2 = 0.68, P < 0.05$) of the variation in staple strength.

Relationship between the body traits and staple strength

Of the body traits, FatCV was the only trait that was significantly related to staple strength ($r = 0.45$) and the only body trait in the multiple regression analysis that significantly explained a proportion (29%) of the variation in staple strength ($r^2 = 0.29$, $P < 0.05$).

Discussion

Mean fibre diameter influences seasonal variation in fibre diameter

Mean fibre diameter is related to the level of variation in fibre diameter along the FDP in grazing sheep. Sheep with higher mean fibre diameter have greater absolute changes in fibre diameter throughout the year. Associated with this, sheep with higher mean fibre diameter also had greater variation in fibre diameter along the staple, changes in fibre diameter that occur over a shorter length of the staple, and greater variation of fibre diameter among fibres. Previous authors have observed that sheep with greater mean fibre diameter have greater variation in fibre diameter throughout the wool growth period (Jackson and Downes 1979; Thompson 1993; Bow and Hansford 1994; Earl *et al*. 1994). Furthermore, Hynd (1992) also observed that initial fibre diameter was positively correlated with absolute change in fibre diameter. In contrast, Adams and Briegel (1998) did not find any evidence to suggest that variation in diameter, measured by variance along fibres, might be correlated with mid-side mean fibre diameter.

The biological causes for these relationships have not been established. As sheep with greater fibre diameter have larger follicles and bulbs (Schinckel 1961; Hynd 1995; Hill *et al.* 1997) they may therefore have a greater capacity to obtain a higher fibre diameter. Alternatively, sheep with follicles that produce finer fibres do not have the physical ability to produce large fibres and as a result do not change fibre diameters as much relative to the broader fibres. Furthermore, mean fibre diameter is negatively correlated with the ratio of secondary to primary follicles (Skerritt *et al*. 1997). Therefore, sheep with higher mean fibre diameter should have a greater proportion of fibres from primary follicles, which have been suggested to be more sensitive in terms of fibre diameter responses to changes in wool growth (Lockart 1956; Onions 1962; Quinnell *et al*. 1973). Furthermore, secondary follicles are more affected by changes in nutrition than primary follicles (Lyne 1964; Ryder and Stephenson 1968) and are therefore more susceptible to follicle shutdown. These results suggest that sheep differing in their ratio of secondary to primary follicles, and therefore fibre diameter, may respond differently to changes in their environment.

Neither average fibre length nor change in fibre length growth throughout the experiment was significantly correlated with mean fibre diameter measurements. Hynd (1992) also found that initial fibre diameter was not significantly correlated with change in fibre length.

The overall effect of increasing initial and mid-side mean fibre diameter on staple strength was not large, with initial mean fibre diameter and mid-side mean fibre diameter being negatively, but not significantly, correlated with staple strength. These results are in contrast to the

Table 5. Correlation coefficients for the relationships between the wool fibre characteristics and staple strength

AvL/D, average ratio of fibre length to fibre diameter over the 3 measurement periods; L/DCV, CV in the ratio of fibre length to fibre diameter over the 3 measurement periods; FGCV, variation in FG between the 3 measurement periods; FDCV, CV in FG between the 3 measurement periods; AvFL, average fibre length; AvFLCV, average CV in fibre length over the 3 measurement periods; △FL, change in fibre length growth between measurements; △FD, change in fibre diameter between measurements; AvSL(bands), the average staple length growth between dyebands; CVSL(bands), CV in staple length growth between dyebands

Characteristics	AvL/D	L/DCV	FGCV	FDCV	AvFL	AvFLCV
Correlation	−0.02	−0.20	−0.23	0.31	−0.17	−0.51*
Characteristics	△FL	△FD	△FL/△FD	AvSL(bands)	CVSL(bands)	
Correlation	−0.31	0.18	−0.47*	−0.10	−0.63*	

*$P < 0.05$.

majority of correlations reported (Hansford and Kennedy 1990; Lewer and Ritchie 1992; Lewer and Li 1994; Greeff *et al*. 1995; Brown *et al*. 1999; Yamin *et al*. 1999), which are generally positive.

L/D Ratio

Differences among grazing sheep in L/D are associated with differences in their responsiveness of fibre diameter throughout the year and therefore FDP characteristics. The influence of L/D on the FDP characteristics is a combination of the influence of fibre length growth and mean fibre diameter. Examining these individually first, sheep with higher average fibre length growth had greater variation in fibre diameter along and among fibres. As detailed above, average fibre diameter was positively associated with variation in fibre diameter along the staple. There was no significant relationship between average fibre length growth and average fibre diameter.

L/D was significantly and negatively correlated with the first rate of fibre diameter change within the FDP. The sheep with higher L/D may alter fibre length preferentially to diameter, resulting in the changes in fibre diameter throughout the year being over longer length of fibre growth and hence lower rates of fibre diameter change. However, L/D was not significantly associated with the overall level of along-staple and between-fibre variation in fibre diameter.

The lack of relationship between L/D and along-staple variation in fibre diameter can be explained by examining how L/D is related to fibre length growth and average fibre diameter. Sheep with higher L/Ds, although having significantly greater fibre length growth rates also had significantly lower average fibre diameters. As fibre length growth and average fibre diameter were both positively associated with along-staple variation in fibre diameter, the increased fibre length growth rate and reduced mean fibre diameter resulting from higher L/Ds appear to counteract each other and result in no significant relationship between L/D and along-staple variation in fibre diameter. This suggests that the relationship between L/D and FDP characteristics is due to both length and fibre diameter, rather than fibre diameter or fibre length alone. When animals were examined within micron group, which removed the influence of mean fibre diameter, L/D was strongly and positively correlated with along-staple variation in fibre diameter.

The relationships between fibre diameter and length may be better described by using independent regression equations for each animal (Scobie and Saville 2000). This would also allow for curvilinear relationships within each animal, i.e. where L/D is not constant across all fibre diameters within an animal. This analysis may help to untangle relationships observed in this study.

The negative relationships between L/D and mean fibre diameter are consistent with the negative correlation observed by Hynd (1992) between initial fibre diameter and L/D. These results confirm that sheep with higher average fibre diameter have lower fibre length growth relative to average fibre diameter.

Sheep with greater L/Ds had slightly smaller changes in fibre diameter among measurements of L/D, greater changes in fibre length among L/D measurements, and a greater ratio of change in fibre length to that of change in fibre diameter. These relationships observed in grazing fine wool Merino wethers strongly agree with those of Hynd (1992) using housed and pen-fed South Australian strong wool Merino sheep. Hynd (1992) also observed that sheep with higher L/Ds had lower increases in fibre diameter, slightly smaller changes in fibre length, and a greater ratio of change in fibre length to that of change in fibre diameter. This author concluded that direct or indirect selection for sheep with high L/D would have the 2 desirable outcomes of greater fibre length and reduced fibre diameter variability. In this experiment, L/D was positively correlated with average fibre length growth and staple length but negatively correlated with most characteristics that describe fibre diameter variation along the staple and among fibres. These results support these previous conclusions, although at a phenotypic level only.

Seasonal variation in fibre diameter and length is related to staple strength

Seasonal variation in fibre length growth, fibre diameter, and the ratio of length to diameter throughout the year is associated with increased variation in fibre diameter along the FDP and reduced staple strength in grazing sheep. All the measures of changes in fibre length growth and fibre diameter throughout the experiment measured at the individual fibre, FDP, and mid-side levels were negatively correlated with staple strength to varying degrees. All these results have illustrated that increasing variation in fibre length growth and diameter throughout the year increases the variation of fibre diameter along the FDP and reduces staple strength.

Variation in fibre diameter and variation in fibre length among fibres were of approximately equal importance in explaining variation in staple strength. Fibre diameter and length tend to change together in response to changes in nutritional conditions (Hynd 1994). Therefore, it is anticipated that sheep with lower variation in fibre diameter among fibres would have lower variation in fibre length. The significant positive correlations observed between mid-side fibre diameter variation and variation in fibre diameter among fibres within snippets with fibre length variation support these theories. Peterson *et al*. (1998) also observed a weak positive relationship among fibre diameter variation between fibres and variation in fibre length. Contrary to these results, Schlink *et al*. (1998) found no significant relationship between variation in fibre diameter and variation in fibre length within a staple. Lower variation in fibre length can result in greater staple strength (de Jong *et al.* 1985; Thompson 1993; Swan 1994; Bray *et al.* 1995; Peterson 1997; Peterson *et al.* 1998). This again was supported in this study, with a significant negative correlation between fibre length variation and staple strength.

This experiment demonstrated that the FDP characteristics are correlated with staple strength and explain additional variation in staple strength above that which could be explained by the measurements of mid-side mean fibre diameter, mid-side fibre diameter variation and staple length. These results agree with those of Brown *et al.* (1999, 2002) and Brown (2000) by illustrating a distinct benefit, in terms of explaining staple strength, of using both mid-side and FDP measurements. The FDP characteristics used alone and in combination with the mid-side measurements explained a greater proportion of the variation among animals in staple strength compared with the mid-side measurements used alone. This confirms the benefits that can be gained by measuring FDPs.

Seasonal variation in body weight and composition

Seasonal variation in body weight, fat depth, and skin thickness is related to variation in fibre diameter along the FDP in grazing sheep. Seasonal variation in body weight, fat depth, and skin thickness was positively correlated with the overall fibre diameter of the FDP, variation in fibre diameter along the FDP, and rates of fibre diameter change throughout the FDP. Variation in skin thickness was the body measurement that was most related to variation in fibre diameter along the FDP. Sheep that had greater seasonal variation in body weight and condition may have altered feed intake and/or metabolism throughout the year, which resulted in increased variation in the availability of nutrients to the wool follicle. As fibre diameter and length growth rates depend heavily on the quantity and quality of nutrients available to the follicle, the increased variation in skin thickness throughout the year may have resulted in greater variations in follicle nutrition and therefore wool growth throughout the experiment. This supports the theories that skin thickness is related to the level of overall sheep nutrition and follicle nutrition (Hutchinson 1957; Lyne 1964; Williams and Thornberry 1992; Williams and Morley 1994; Schlink *et al.* 1996*b*). Although these body characteristics were correlated with variation in fibre diameter along the staple, they explained less overall variation in the FDP characteristics than the fibre-based measurements.

Despite the positive association between seasonal variation in body weight and condition and fibre diameter variation along the staple, sheep that showed greater variation in body weight and fat depth throughout the experiment also tended to have stronger wool. In contrast, sheep that showed greater variation in skin thickness tended to have reduced staple strength. The positive association between seasonal variation of body weight and fat depth and staple strength may indicate that some animals partition more nutrients towards the skin and therefore wool growth when nutrients become limiting rather than maintaining body weight and fat depth. However, these relationships were not a result of reductions in variation in fibre diameter along the staple but rather reductions in the variation in fibre diameter and length among fibres. Seasonal variation in body weight and fat depth was negatively associated with variation in fibre diameter and length among fibres, whereas seasonal variation in skin thickness was positively associated with variation in fibre diameter and length among fibres. These results indicate that the reduced variation in skin thickness throughout the year may have resulted in less variation in nutrient supply to the follicle and therefore reduced variation in fibre diameter and length among fibres, which was both significantly and negatively correlated with staple strength.

Seasonal variation in body weight was not significantly correlated with either variation in fat depth or variation in skin thickness. Williams and Thornberry (1992) also found that skin thickness was not significantly related to either liveweight or body condition score. Seasonal variation in fat depth and skin thickness was also not related. These relationships further indicate that body weight, fat depth, and skin thickness follow different seasonal patterns throughout the year.

Furthermore, sheep with thicker skins have less variation in fibre diameter along the FDP but greater fibre diameter, fibre length growth, and variation in fibre diameter and fibre length among fibres. The greater skin thickness may indicate that the follicles of the sheep with greater skin thickness have improved nutrition to express a higher wool growth and therefore fibre diameter and length variation among fibres. The thicker skins may also provide a buffer of nutrient reserves for when nutrients become limiting and hence less variation in fibre diameter along fibres.

Despite finding significant differences in the level of variation in wool growth and fibre diameter patterns throughout year, Adams and Briegel (1998) found no significant differences among 3 strains of grazing Merino wethers in the pattern of liveweight change throughout the year. Furthermore, there were no significant relationships between wool growth rate and either loss of lean or loss of fat. There have been no other published studies of the relationship between seasonal variation in body weight and condition and FDP characteristics. Adams and Briegel (1998) also rejected the hypothesis that the large sheep could buffer wool growth throughout the year by mobilising body reserves. The fact that in the present study average body weight and fat depth were non-significantly correlated with the level of fibre diameter variation along the FDP supports these previous findings. However, mean skin thickness and seasonal patterns of body weight, fat depth, and skin thickness were related to both variation in fibre diameter and length growth among fibres.

Seasonal variation in L/D

The three L/D measurements during this experiment were all highly correlated. The second L/D measurement was also significantly higher than the first L/D measurement. These results indicate that although there is seasonal variation in L/D measurements, the animals maintain their rankings on L/D. These results agree with those of Hynd (1992) who found that L/D was highly repeatable with nutritional change ($r = 0.95$). Schlink *et al*. (1996*a*) and Woods and Orwin (1988) observed significant seasonal variation in L/D in grazing sheep throughout the year, and also noted that despite the seasonal variations in L, D, and L/D the ranking of the animals for these characteristics remained similar throughout the experiment.

Conclusions

Differences among sheep in fibre length, diameter, and L/D are associated with differences in FDP characteristics. Mean fibre diameter of the sheep has a strong influence on the levels of variation along and among fibres; however, sheep can be identified that have similar levels of mean fibre diameter but markedly different levels of variation of fibre diameter along the staple. Within sheep of similar fibre diameter there was a strong positive relationship between fibre length growth rate and L/D with along-staple variation in fibre diameter. Seasonal variation in fibre length and diameter growth increased the variation in fibre diameter along the FDP and reduced staple strength. Seasonal changes in body weight, body condition, and skin thickness can be related to changes in fibre diameter and length among fibres, fibre diameter along the FDP, and staple strength. The influence of body weight and fat depth on wool growth was different to that of skin thickness.

As this study only involved 16 sheep, a larger study is required using more sheep of different genotypes over a number of environments to confirm these relationships. However, the technique required to calculate L/D is very time consuming and expensive. Therefore, it would be beneficial if the technique could be modified to make estimation of fibre length more practical.

These relationships are complex and much research is required to fully examine how these characteristics combine to influence variation in fibre diameter throughout the year and staple strength. With further research, variation in fibre diameter, length, and L/D might be able to be used in combination with FDPs, wool quality characteristics, and body traits to reduce seasonal environmental responsiveness of fibre diameter.

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