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Hypothesis for How Linear Glutenin Holds Gas in Dough

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ABSTRACT

A hypothesis is put forward to explain how dough resists uncontrolled expansion of gas cells. Hand kneading, mixer action or gas pressure shears swollen protein in dough. Shearing orients linear glutenin molecules parallel to the shearing forces. Molecules with little overlap are pulled apart in the shear gradient, giving them further chances of getting better overlap with other molecules. Mixing thus forms a well overlapped and coherent gluten. When starch granules are pressed together the protein phase between them gets squeezed out sideways and so undergoes shear at angles of up to 90° to the main direction of flow. A similar result is found if the swollen protein suspension is regarded as being pressed through the tortuous pores between granules: since there will be flow in every pore, the gluten is sheared locally parallel to the pore direction. The pores between starch granules form a continuous three-dimensional network; therefore the protein also forms such a network, which appears isotropic because the orientation is local.

Unless a gluten is weak, bubbles can expand without bursting because this network of protein resists forces in all directions until gelling of starch sets the crumb structure; further expansion then tears the starch/protein matrix enough to release the pressure in the bubbles.

Elasticity does not arise from stretching the bonds of polypeptide chains but because folded conformations of chains are incomparably more probable than unfolded ones. Brownian motion helps unfolded chains to refold rapidly.

Relaxation during normal proof times, while letting unfolded chains refold, does not destroy all orientation and overlap.

Part of the action of fungal α-amylase may be to widen the pores between starch granules, reduce the size of small granules that could block such pores and delay starch gelation by slowing the entry of water. Fat could ease the relative movement of granules and protein, and the work of expanding gas cells. The fibrils seen when flour particles are wetted may illustrate the effects on glutenin of shear, produced in this case by sudden release of osmotic pressure.

Moulding by sheeting gives an overall direction of orientation (DO) lacking in newly mixed dough. For the surfaces of a rolled sheet this DO lies in the machine direction, but inside the sheet it is sideways. In one-piece bread the asymmetry of gas cells results from easier expansion in the main DO, i.e. along the loaf. In four-piece bread the lack of room to expand horizontally forces cells to elongate vertically.

INTRODUCTION

Glutenin, forming roughly 5% of a bread flour of 11% protein, is the protein that gives dough its viscoelasticity. Three hypotheses predicting that glutenin molecules are linear arrays of chains have been put forward (Ewart, 1968; Bernardin & Kasarda, 1973*a*,*b*; Khan & Bushuk, 1978). It is not easy, however, to see how linear molecules can enclose expanding gas bubbles, which exert tangential forces at their surfaces. To make a sheet that would be strong in all directions, as in the fabric of a balloon, molecules would need to be interwoven as intimately as fibres in cloth, which is most unlikely.

This paper tries to explain how dough holds gas cells.

The word chain means glutenin subunit throughout.

HYPOTHESIS

Wetting protein

Storage proteins are laid down in protein bodies, the molecules being probably close-packed because this would save space and be favoured by evolution. In the mature seed, protein bodies have coalesced to form packets of protein, mostly 10 to 30 μm across (Jones *et al.*, 1959). Water will not only fill the gaps between molecules, which are rather like the spaces between close-packed uniform spheres, but will compete with touching protein molecules for the polar groups involved in these contacts. Gliadins or low oligomers of glutenin will only be sparingly soluble in dough liquor (~0·5M NaCl).

Water associated with gluten

The fraction of space in close-packed uniform spheres is $(1 - \pi/\sqrt{18}) = 0{\cdot}259\,52$. If chains were spherical, with mol. wt 50 000 and density 4/3, their diameter would be 4·9 nm. The water content (w/w) of the whole system could be 21% if there were no swelling. Proteins probably suffer some distortion of structure on going from the wet to the air-dry state (see p. 254 of Kuntz & Kauzmann, 1974), but this would presumably disappear on wetting. Estimates of the water in dough associated with 1 g of dry protein range from 1·1 g (Greer & Stewart, 1959) to 2·15 g (Bushuk, 1966). These amounts would form a sheath 4 to 6 water molecules thick on average round a glutenin molecule, assuming it to be a straight row of uniform spheres. The mean distance apart would be twice the sheath thickness, 8–12 molecules, implying that all glutenin would be in solution. Since even washed-out gluten, which is $\frac{2}{3}$ water (w/w), is not a solution, glutenin molecules will often touch one another along their lengths in the swollen packets of protein. This will lead to cooperative association, where contacts help adjacent contacts to form by restricting freedom.

Shearing

Whether dough is squeezed or pulled, Figs 1 and 2 show that it is sheared.

If a dough piece (~400 ml) were spread over the area swept out by the outer edges of the blades of a Morton mixer in the Chorleywood Bread

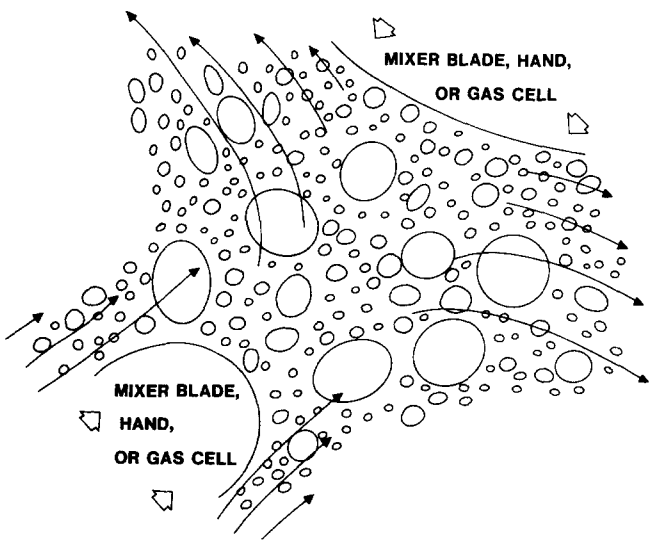

Fig. 1. Squeezing dough causes shearing.

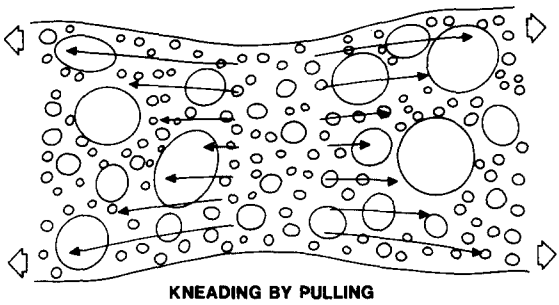

Fig. 2. Pulling dough causes shearing.

Process (CBP) with a work input of $40\,Jg^{-1}$ dough, it would only be $\sim 9\,\mu m$ thick, i.e. in the range of starch granule diameters or $\sim 1800\times$ the diameter of a chain. This shows that thorough shearing takes place in the CBP. It is easy to see how shearing arises in pores between starch granules when they are parallel to the shearing forces. What is not so obvious is that, as these forces press granules together in trains, the protein is squeezed out sideways, which means it must be sheared in all pores, whether parallel to the shear forces or not.

Shear turns molecules into the direction of shear

Figure 3(a) shows a molecule lying across shear planes, each part travelling at the speed of the plane it is in. If the speeds are replotted relative to the centre of mass, C, (Fig. 3(b)) it is clear that the molecule is being turned to aline it in the shear direction.

Shearing strips molecules from protein bodies

Drying the grain probably compacts the protein bodies. These may separate during wetting and mixing. If this does not happen, the words 'protein packet' should be read for 'protein body' in the following.

At high shear gradients, e.g. near mixer blades, protein bodies probably undergo some disturbance of packing (Fig. 4(a) & (b)). Well oriented glutenin in a protein body would probably resist shearing along its direction of orientation (DO) because all secondary forces holding a molecule to its neighbours would have to be broken simultaneously to free it, whereas they would break in succession if the shear direction crossed the DO since only the forces holding one chain need be broken at a given instant. (If the packing in protein bodies is more complicated than the stylised Fig. 4 implies, with molecules folded back on themselves or intertwined, the following explanation should still apply in general.)

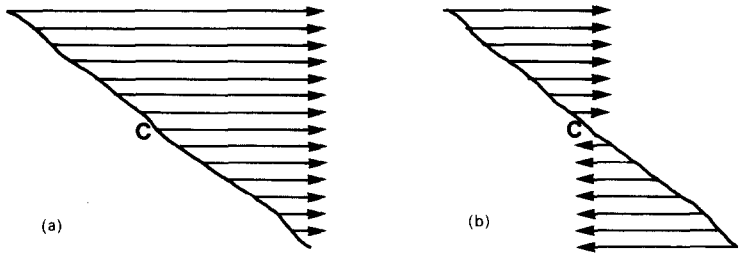

Fig. 3. (a) Velocities of a glutenin molecule lying across shear planes in dough. (b) Plotting velocities relative to centre of mass (C) shows that the molecule is turning to become parallel to the direction of shear.

During mixing, when a protein body was overtaken by faster molecules or starch granules, these would make transient contacts with it. Especially where two or three chains protruded from the mass, the forces between these and overtaking molecules would often be stronger than those holding the first bound chain and would pull it free (A, Fig. 4(c), (d) & (e)). The section gripped plus the freed chain would make strong enough contacts with the faster stream of molecules to continue the process, chain by chain, till the whole molecule was free; the process becomes easier as further chains are dislodged, because their combined secondary forces more and more strongly outweigh those holding a chain to three neighbours at most. (Figure 4 is, of course, two dimensional. A close-packed protein molecule in a packet ideally has six neighbours (Fig. 5), but this falls to three for a surface molecule, or two for a more exposed one. The foregoing argument, however, is valid in a real dough because in the protein body the three molecules holding the one being removed (A) are countered by the three overtaking molecules.)

This explanation suggests that molecules overtaking a protein body with good internal orientation but no protruding chains cannot get enough grip on molecules to peel them off. One reason that the CBP is so effective is its

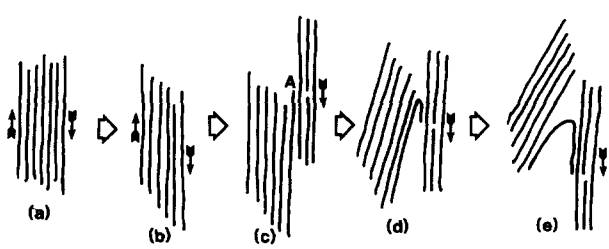

Fig. 4. (a) and (b) Shear may disturb well oriented molecules in protein bodies and make them vulnerable to stripping. (c), (d) and (e) When a surface molecule protrudes, as at A, it can be removed easily, since weak secondary forces need only be broken one at a time to free it.

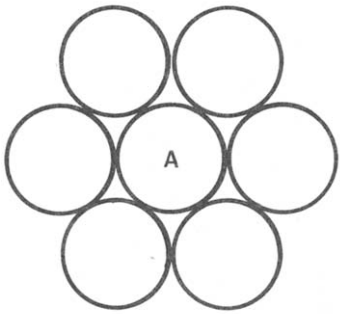

Fig. 5. A well oriented glutenin chain A can have six neighbours.

vigorous shearing. The behaviour in industry of added glutens may be influenced by particle size as well as the length of their glutenin molecules. Material that cannot be stripped and overlapped will be ineffectual for breadmaking. Clearly, work input will be an important factor here.

Distribution of glutenins and gliadins

Since dough has as much gliadin as glutenin the problem of how they are distributed arises. Cross sections drawn with regular arrangements of glutenin and gliadins not only looked improbably neat but at best gave monomolecular films of glutenin. When a matrix of 225 close-packed circles was drawn (Fig. 6) and half were assigned to glutenin by using random numbers, the distribution looked more plausible because there is association of glutenin to fibres even on this very small scale. Some of the smallest pores

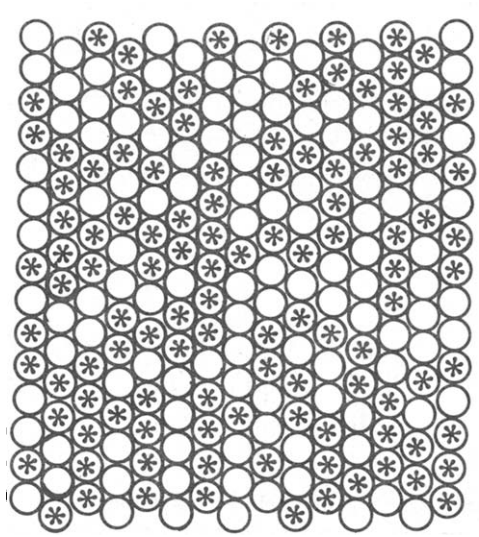

Fig. 6. 112 circles ⊛ in a close-packed array of 225 chosen with random numbers.

in dough (between B starch granules of diameter 1 μm) would at their narrowest just take a circle of diameter equal to the granule diameter $(D) \times [(2/\sqrt{3}) - 1] = 0{\cdot}154\,7D$, the circle holding about 450 glutenin molecules and an equivalent number of gliadins. (This formula also shows that not many B granules could pass through the pores in a layer of A granules.)

It is therefore suggested that when glutenin molecules associate in fibres, substantial numbers of gliadins are found alongside them. It is also possible that gliadins could clump together, behaving rather like very small unstable starch granules. The 1–2 × excess of unbound water over protein must be trapped in capillaries formed by glutenin fibres and aggregates of gliadins, and probably helps lubricate the movement of fibres over neighbouring fibres and granules. It is also conceivable that gliadins not only act as cross-bridges aiding cohesion, but help molecular slip, acting analogously to ball bearings. To get at least a qualitative idea of the way the water is dispersed, Fig. 6 can be looked at again, but this time taking the filled circles as glutenin or gliadin and the clear circles as water.

Cohesion depends on overlap

If molecules were oriented as in Fig. 7(a), the strength would be negligible, depending only on weak secondary forces between the tips of molecules. Obviously, the greater the overlap (Fig. 7(b)) the more the strength rises, up to a limit when combined secondary forces are stronger than covalent bonds, which then begin to fail. If all the molecules were the same size, optimum strength would occur when the overlap was half the length with regular arrangement (Fig. 7(b)). The Appendix shows that the mean overlap in a random arrangement is half the molecular length for uniform molecules. In practice most polymers vary widely in length. An average overlap of half the length means that some molecules have poor contacts with their neighbours, which will break during mixing and the molecules will slip to new positions. For the longer molecules on which strength depends, about half these random overlaps will be strong, i.e. at least half the length (Appendix). Weak

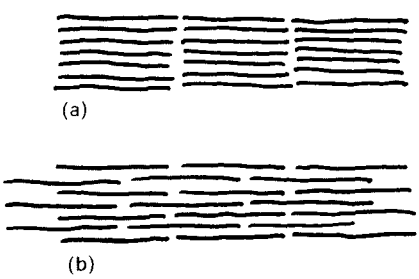

Fig. 7. (a) Good orientation without overlapping cannot give strength. (b) Orientation and overlapping by half the length of uniform molecules gives maximum strength.

overlaps will again be broken giving another 50:50 chance of finding good overlap. In this way mixing improves the strength of dough by bringing about efficient overlapping. The process illustrates Le Chatelier's principle because the protein is reoriented to resist the applied forces of mixing.

Though orientation by very strong shearing actually causes viscosity to decrease, the drag, or tangential stress, still increases (though not as fast as it would have done if the liquid were Newtonian). If the shear field is weak enough, it cannot overcome the disorienting effect of Brownian motion and the dough becomes 'unmixed' (Tipples & Kilborn, 1975; Parades-Lopez & Bushuk, 1983).

Elasticity not due to bond stretching

Elasticity of polymer chains is not, as has been said, due to stretching the main chain. Such a view is plausible because Morse potential energy curves show that bonds can stretch to about five times their length at high energy, which would be enough to explain the stretching of rubber, gluten, etc. Many advanced textbooks throw no explicit light on this point. The fallacy is exposed, as it so often is, when treated quantitatively.

The vibration frequency of polymer bonds is of the order of $10^{13}\,s^{-1}$. If therefore a bond of a chain was extended by stretching, then 5×10^{-14} s later it would contract. Therefore bond stretching could not cause any practical extension of a polymer, which would have to last for several orders of magnitude longer than this. Again, bonds should stretch and contract alternately along the polymer chain with little overall change of length.

Cause of elasticity

The logic behind the 2nd Law of Thermodynamics (in any spontaneous change the entropy of the universe increases) is that any *particular* distribution of particles or energy quanta is as likely as any other. The ways in which matter can be arranged in ordered patterns (e.g. stretched polymer chains) or excess quanta can be confined in high energy bonds or restricted to a few particles in a system are incomparably fewer than either the number of disordered patterns (e.g. folded conformations) or the distributions of quanta among a larger number of particles.

Therefore what is always seen in practice after a spontaneous change is the likeliest distribution, e.g. a folded polymer chain or the widest sharing of energy quanta. Consequently, all spontaneous reactions are entropy-driven, though the term tends to be used only where particles, not quanta, are redistributed.

When the central chains of glutenin molecules are unfolded into one of a

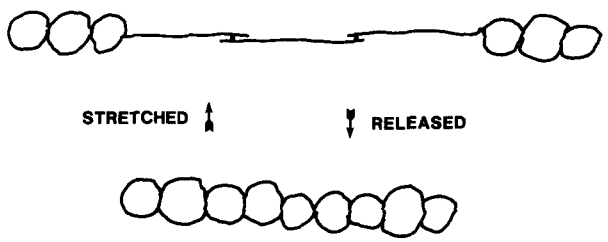

Fig. 8. Glutenin molecule contracts on release of stress, while tending to retain its orientation in space.

small number of possible conformations and then released, Brownian motion ensures that vastly more probable folded conformations are rapidly reached, by frictionless rotations about all the links in the peptide chain except the actual peptide bonds and the αC–N bonds in proline (Fig. 8). Refolding times for protein chains are of the order of 1 s but steric hindrance would probably delay the refolding of glutenin chains in dough. Bloksma (1981) said that the relaxation time of dough is of the order of 10 s, which is compatible with chain refolding being the basis of dough elasticity.

Difference from original hypothesis

In a paper on a linear glutenin hypothesis (Ewart, 1968) it was stated that there was 'orientation of the linear glutenin molecules in all directions', to

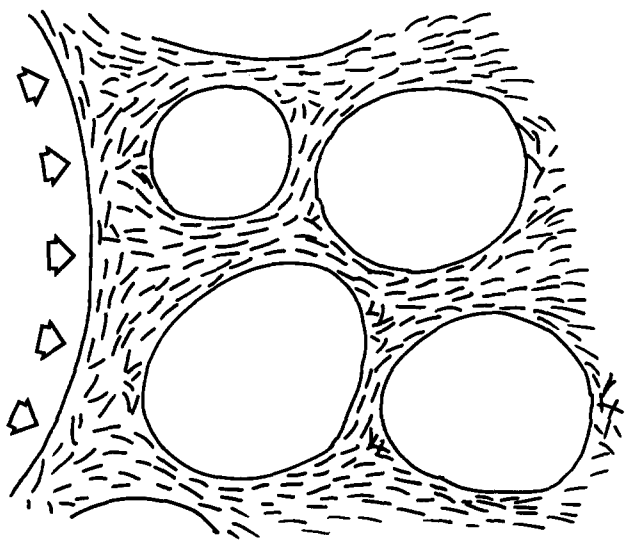

Fig. 9. Stylised sketch of how glutenin molecules are oriented in the channels between even the smallest starch granules (diameter ~ 1 μm). Lengths of glutenin molecules are roughly on the same scale.

give a viscoelastic structure. This argument is flawed because the contacts between molecules that cross one another at random would be too slight to give dough enough strength. The modification introduced here is that swollen protein forms a three-dimensional network in the pores of varying cross section that lie between starch granules, and it is orientated and overlapped parallel to the direction of each pore, even the narrowest (Fig. 9). (In the narrowest parts of a pore the shear is strongest and so gives the best orientation. This tends to compensate for the narrowness of the fibre at this point.)

Bloksma (1981) said there are $1{\cdot}5 \times 10^{11}$ gas cells in $1\ m^3$ of non-gaseous dough. Calculation from data of Soulaka & Morrison (1985) gives $3{\cdot}4 \times 10^{15}$ starch granules in $1\ m^3$ of non-gaseous dough. Since there are $>20\,000$ granules to each gas bubble, there are likely to be many pores filled with protein and oriented in different directions between any two gas cells. This system therefore resists tangential stresses at the cell surfaces.

RELATED TOPICS

Surface tension

Carlson & Bohlin (1978) calculated that $\sim 80\%$ of the elastic energy used in expanding dough was lost in opposing surface tension. Bloksma (1981) disagreed with this but concluded that a greater pressure in gas cells was needed to overcome surface tension than viscous resistance of the dough. Owing to the simplifying assumptions that were made, however, it is difficult to know how valid the conclusions are.

Obviously, there is enough pressure in gas cells to overcome surface tension or the dough would not expand. In a given dough it is unlikely that a change in the mol.wt of glutenin will affect surface tension much, but it will have a large effect on viscous resistance. Therefore, though emulsifiers may increase loaf volume by reducing work done against surface tension, the viscosity of a *given* dough is largely governed by the state of the glutenin (its mol.wt, and whether it has been well oriented and overlapped), and it is this that decides whether cells can expand satisfactorily. Some doughs are too strong to give adequate expansion. A too weak dough could not prevent its being squeezed from between gas cells, which then join to give a coarse structure: in severe cases the gas cells could even burst, become continuous and allow the pressure to escape. If this happens before the starch has gelled enough to set the crumb structure, the loaf collapses. After gelation sets the crumb structure, any more expansion ruptures it and connects the gas cells, so releasing their pressure: on cooling, as steam condenses in them, air can flow in and stop the loaf collapsing.

Fungal α-amylase

P. E. Pritchard (1986, pers. comm.) has shown that the bread-improving action of large additions of fungal α-amylase (FAA) preparations is due to amylase itself. He suggested that the first starch granules to gel are digested so that the dough remains fluid longer and thus expands further.

He found that FAA raised the amount of reducing sugars by $\sim 10\,\mathrm{mg\,g^{-1}}$ of wet dough on average in two flours compared with the controls: one flour had high starch damage and the other, low.

When a weight of maltose is converted to the weight of starch it came from, by the factor 0·947, then divided by 0·45 (the weight fraction of starch in dough) it is seen that FAA digested an extra 2·1% of the starch.

Starch occupies ~57% of the volume of non-gaseous dough, so the pores take up 43%. Let V be the volume of non-gaseous dough, then 2·1% of the $0{\cdot}57V$ occupied by starch is lost. This loss increases the pore volume by $(2{\cdot}1 \times 0{\cdot}57V \times 100)/(100 \times 0{\cdot}43V) = 2{\cdot}8\%$, i.e. multiplies it by 1·028.

FAA would not increase the length of the pore network but only the mean diameter, P. Since volume at constant length is proportional to P^2, P increases by a factor $\sqrt{1{\cdot}028} = 1{\cdot}014$.

Shearing of non-gaseous dough during loaf expansion causes flow of swollen protein through the pores, and flow of granules through protein. Since granules moving through protein can be seen as protein flowing between granules simply by considering the motion relative to the granules, all the flow may be taken as movement of protein through pores. The rate of flow is proportional to P^4, by Poiseuille's law, so FAA should increase it by $(1{\cdot}014)^4$, or 5·6%.

Such an increase in flow rate would also appear as a decrease in dough viscosity. Pritchard (1986, pers. comm.) observed both these changes to be significant.

Calculation from data on 85 flours (Cauvain & Chamberlain, 1988) gave a mean value of 13·8% (range 1·7 to 23·9%) for the increase in gas cell volume due to FAA. Since flow goes on for longer when FAA is present, the calculated flow due to FAA should be more than 5·6%. The fact that it is of the order of the mean experimental value suggests that this mechanism may be part of the improving action of FAA.

During flow, pores could be blocked at their narrowest parts by small granules. (In a system of close-packed uniform spheres of diameter D, the diameter of a ball that just fits the pore varies from a maximum of $0{\cdot}225D$ (i.e. $D(\sqrt{\frac{3}{2}} - 1)$) to $0{\cdot}155D$.) FAA is likely to be particularly effective in reducing the size of such small granules owing to their large surface to mass ratio.

These granules are probably the first to gel. If, as Pritchard suggested, they

are removed early, this would unblock pores and help flow more effectually than if the loss of starch is assigned solely to raising the average pore diameter.

The loss of starch means that as starch granules swell during baking they have to bridge an enlarged gap before they can meet and then mesh firmly to set the loaf. This also favours a longer expansion time.

Though Pritchard showed that added maltose was ineffectual in increasing loaf volume, it is possible that, when FAA and β-amylase produced *local* concentrations of soluble carbohydrate at the surface of the granules, the osmotic effect would delay diffusion of water into granules at the gelation temperature where water would break their cooperating H-bonds rapidly: such delay could also give the loaf more time to expand.

Fat in the Chorleywood Bread Process

At least 0·7%, based on flour weight, of a fat that will not melt during proof is necessary for good loaf volume in the CBP. Assuming the cross-sectional area of a triglyceride molecule to be three times that of a hydrocarbon chain, which is given as $0{\cdot}3 \times 10^{-18}\,m^2$ (Larsson, 1986) and, calculated from data of Soulaka & Morrison (1985), the surface area of starch in 100 g of flour to be $29\,m^2$, a monolayer of fat on the starch surface would need $3{\cdot}2 \times 10^{19}$ molecules. Since there are $4{\cdot}7 \times 10^{20}$ molecules in 0·7 g of fat there are ~ 7 times enough to form a lipid bilayer over the starch. CBP mixing may disperse fat fairly well in the dough. Owing to its low surface tension, the melted fat could perhaps penetrate between the aqueous protein layer and the starch to form a lubricating bilayer. This may also retard the passage of water into starch, so delaying gelation and giving time for further loaf expansion. Another well known possibility is that a monolayer of lipid forms on the surface of gas cells and reduces the surface tension and work of expansion. If there is enough lipid to coat granules there is enough to coat gas cells.

Wetness of overmixed dough

When glutenin molecules are broken by overwork, reducing agents or proteases, the fibres are very weak because the overlap is so much less. As the overlap is small, there is little chance of central chains being unfolded and so the dough loses elasticity. It flows easily because the short molecules and fibrils are held together by fewer forces. The normally continuous capillaries, which trap water, often have their walls ruptured in such a dough and the water leaks out sideways. This may explain why these doughs feel wet and sticky.

Another possible cause of wetness is that, in a normal dough, orienting is by no means perfect, owing to the steric hindrance that long molecules suffer when they are stripped off and alined by shear. Shortening the molecules may considerably help the clumping of glutenin, which then has fewer internal cavities for holding water.

Fibrils

When flour particles are wetted under a microscope, they rapidly extrude filaments (Bernardin & Kasarda, 1973*a*). The swollen outer layer of protein acts as a semipermeable membrane and the solution of any soluble matter inside, such as albumins, develops osmotic pressure. This pressure is released at the weakest point in the outer layer and the outrush of solution shears the adjacent glutenin into fibrils. This illustrates how the orienting, stripping and overlapping brought about by mixing forms fibrils. The speed of the process is due to the minuteness of molecular dimensions.

Moulding

Moulding, as shown in Figs 1 and 2, causes widespread shearing in the pores between granules and so restores orientation and overlap lost by Brownian motion during resting. It can bring about an overall orientation in a newly mixed dough, just as a tuft of isotropic cotton wool can be partly oriented by pulling. In the second moulding where the dough is sheeted before being rolled up, there is obvious shearing, and hence orientation, in the direction of travel. Since there is sideways flow as well, however, there must be orientation in that direction also. Therefore sheeting produces a DO parallel to the direction of moulding on the surfaces, and at 90° to this in the inner layers.

Moulding and shape of gas cell

When a bubble expands it forces gluten outwards through pores, and granules through viscous gluten. But in addition it has to do work against the molecules surrounding it. Since a bubble should find less resistance when expanding along a DO than at 90° angles to it, there should be preferential expansion of gas cells, or tunnelling, along the DO. (As it grows parallel to the DO it has to part local secondary forces, chain by chain (Fig. 10a). When it grows at 90° to the DO it has to break cooperating secondary forces (Fig. 10b).)

In four-piece moulding the sides of the pan prevent horizontal expansion and gas cells elongate vertically (Collins, 1982), even though the general DO is horizontal and across the pan.

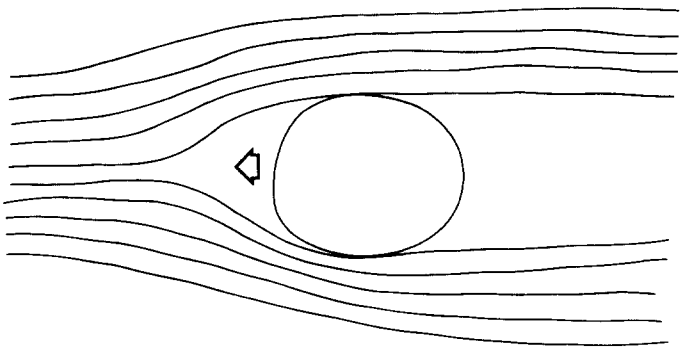

Fig. 10a. Gas bubble expanding parallel to the DO can break secondary forces in succession. Lines denote DOs.

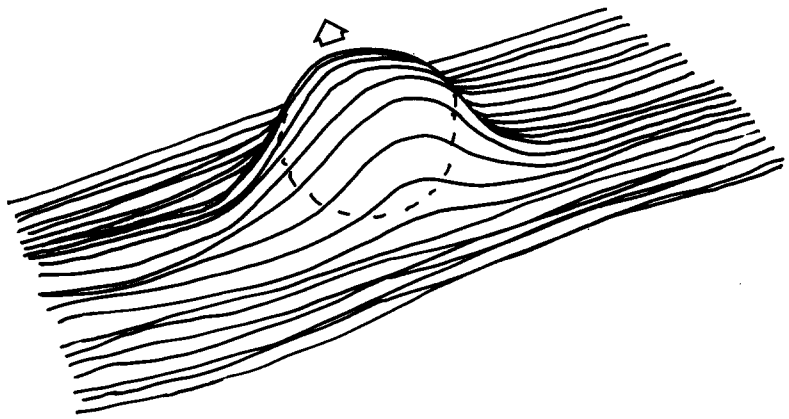

Fig. 10b. Gas bubble expanding at 90° to the DO is restrained by cooperating secondary forces.

In one-piece moulding the dough can expand sideways as well as upwards. The DO of the body of the rolled sheet is parallel to the pan length, hence the observed cell elongation lengthways (Collins, 1982). 'Moulding swirl', seen on the cross section of a one-piece loaf, may be due to the DO (and hence bubble direction) being parallel to this cross section where the surfaces of the dough sheet are, but at 90° to it in most of the cross section.

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APPENDIX: AVERAGE OVERLAP BETWEEN NEIGHBOURING MOLECULES

Any position of overlap of two molecules, lengths i and $j (i < j)$, is assumed equally likely. All possible positions of overlap lie in a distance $i + j$. The chance of an overlap of x is $\mathrm{d}x/(i + j)$. It is easily seen that as one molecule

moves past the other, x increases steadily from 0 to i, remains constant at i for a distance of $j-i$, then decreases steadily from i to 0. Thus

$$\text{average overlap} = 2\int_0^i \frac{x}{i+j}\,dx + \frac{i(j-i)}{i+j}$$
$$= \frac{i^2}{i+j} + \frac{ij-i^2}{i+j}$$
$$= \frac{ij}{i+j}$$

Thus overlap is $\sim\frac{1}{2}$ the molecular length when $i \simeq j$.

If a molecule (length i) is removed by another (length j; $i<j$) by a peeling mechanism (Fig. 4), the overlap is x if the end makes first contact up to $x=i$, and i thereafter. Thus

$$\text{mean overlap} = \int_0^i \frac{x}{j}\,dx + \frac{i(j-i)}{j}$$
$$= \frac{i^2}{2j} + \frac{i(j-i)}{j}$$
$$= i(2j-i)/2j$$

This approximates to half the molecular length for fairly uniform molecules. If $i>j$

$$\text{mean overlap} = \int_0^j \frac{x}{j}\,dx$$
$$= \frac{j}{2}$$