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Oat agriculture, cultivation and breeding targets: implications for human nutrition and health

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Abstract

Oats are undervalued in comparison with wheat, rice and barley, despite their unique composition that includes many of the nutrients required for health and a reduced risk of degenerative disease incidence. Furthermore, oats as whole grain and some of their associated products also contain β -glucan, a complex polysaccharide that has an approved health claim to reduce blood cholesterol levels and reduce the risk of CHD incidence if consumed at ≥ 3 g/d. At the agronomic level, oats exhibit optimal growth in regions of moderate temperature and long day length. In addition, they can tolerate wet weather and acidic soils more effectively than other cereals, such as wheat. Studies have shown that there is diversity in the content and composition of nutrients and health-beneficial components within the available wild and cultivated germplasm and that these are amenable to be enhanced by different agronomic practices as well as are susceptible to climatic variation. The advances in modern plant genetics, developed in sister cereals such as wheat, rice and barley, mean that oat development and exploitation should see an acceleration in the coming decade as they are adopted and applied. These advances include approaches such as genome sequencing, genotyping by sequencing and the allied next-level analytical approaches of RNA sequencing, transcriptome profiling and metabolomics. The collation and coordination of these approaches should lead to the generation of new, tailored oat varieties that are nutritionally enhanced and contain a greater proportion of health-beneficial components that can be translated through into a wide(r) range of consumer products with the ultimate hope of associated benefits to human health and nutrition.

Key words: Oats: Grains: Cereals: β -Glucan

In the preface to his seminal book on oats, Welch⁽¹⁾ states that 'Oats have been likened to Cinderella, an attractive and productive servant, wholesome and dependable, almost thriving on neglect and disinterest, but overshadowed by more assertive if less attractive step-sisters. (O)ats remains a uniquely versatile crop and, like Cinderella, combines an air of robust romance with a powerful potential'. This truism will be expanded upon here and the case made for the future oats with respect to their place in agriculture and human nutrition as well as the consequences for oat breeding and the agrifood chain.

Oats (*Avena sativa* L.) have a long history of use as a nutritious foodstuff, with records suggesting that oats in a cultivated form have been in use since the Bronze Age⁽²⁾. They are a palatable and nutritious foodstuff, mainly supplying carbohydrate in the form of starch and with reasonably high lipid levels (Table 1). Furthermore, oats contain small quantities of several of the B vitamins, particularly thiamin, folic acid, biotin and pantothenic acid, and the protein contains a good balance of essential amino acids. Wholegrain products are significant contributors to our micronutrient intake, and oats

are a good source of Mn, Mg, Se and Fe, as well as Ca, Zn and Cu⁽¹⁾. In addition, oats are by far the predominant source of the soluble fibre β -glucan relative to other grains. Indeed, β -glucan (oat and barley) is the basis of the Food and Drug Administration (USA)⁽³⁾ and Joint Health Claims Initiative (UK)⁽⁴⁾-approved health claims highlighting this component's (and therefore oats') ability to reduce blood cholesterol levels and the risk of CHD incidence (see Box 1, Stewart *et al.*⁽⁵⁾ in this Supplement). The underpinning basis and extent of the impact of β -glucan on CHD are dealt with by Thies *et al.*⁽⁶⁾ and the consequences of processing on oat nutritive and health-beneficial values by Decker *et al.*⁽⁷⁾.

The fundamentals of oat biology with respect to grain biology and nutrient and health-beneficial component localisation are outwith the scope of this brief review of oat cultivation, agriculture and breeding, but are admirably covered by Miller & Fulcher⁽⁸⁾. Briefly, oats can be divided into two classes – hulled, comprising a groat enclosed in a hull, and naked, where the hull is lightly attached but lost during threshing – with the latter (hull-free oats) deemed nutritionally superior to the former. The hull is largely composed of non-nutritive or

Abbreviations: DArT, diversity array technology; MW, molecular weight; N, fertiliser nitrogen.

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Table 1. Nutritional composition of oatmeal and wholemeal wheat flour*†

Nutrients	Oatmeal (100 g)	Wholemeal wheat flour (100 g)	Oatmeal (40 g)	Wholemeal wheat flour (40 g)
Energy				
kcal	401	310	160	124
kJ	1678	1297	669	519
Protein (g)	12.4	12.7	5.0	5.1
Oil (g)	8.7	2.2	3.5	0.9
Carbohydrate (g)	72.8	63.9	29.1	25.6
Dietary fibre (g)	6.8	9.0	2.7	3.6
K (mg)	370	340	148	136
Ca (mg)	55	38	22	15
Mg (mg)	110	120	44	48
P (mg)	380	320	152	128
Fe (mg)	4.1	3.9	1.6	1.6
Cu (mg)	0.23	0.45	0.09	0.18
Zn (mg)	3.3	2.9	1.3	1.2
Se (µg)‡	8.6	9.5	3.4	3.8
Vitamin E (mg)	1.7	1.4	0.7	0.6
Thiamin (mg)	0.50	0.47	0.20	0.19
Riboflavin (mg)	0.10	0.09	0.04	0.036
Niacin (mg)	3.8	8.2	1.5	3.3
Vitamin B ₆ (mg)	0.12	0.50	0.05	0.2
Folic acid (µg)	60	57	24	23

* Data taken from Welch⁽¹⁾ and the US Department of Agriculture Nutrient Database⁽⁵⁶⁾.

† The 100 and 40 g columns aid in interpretation with respect to labelling; normally 100 g is used as a standard amount against which nutritional content labelling is used and 40 g is a common suggested serving amount for oatmeal.

‡ 14.0 µg/100 g – content is variable depending on soil and fertiliser regimen.

putatively anti-nutritive components such as hemicellulose, cellulose and lignin⁽⁹⁾, and the increased nutritive value of the naked oats is due to a proportional weight difference basis because of the absence of a hull.

Cultivation and production

Oat is a crop produced on a global scale, but not at the level exhibited by what can be considered as staple crops, such as maize, rice, wheat, barley and millet (Fig. 1). The latest complete set of figures from The Food and Agriculture Organization Corporate Statistical Database (faostat.fao.org) indicate that in 2012 the global oat production was 19.6 megatonnes⁽¹⁰⁾. The US Department of Agriculture⁽¹¹⁾ posted a preliminary figure of about 23.6 megatonnes for the 2013/2014 global oat production, a 10.6% increase over the 2012/2013 harvest. These production data indicate a significant reduction on the global total of 46.9 megatonnes in 1961 and are indicative of a progressive decrease in global production (Fig. 2). However, this trend is perhaps a composite of several factors: the lack of development of oats into multiple products (being addressed only now) combined with the dominance of wheat and barley. Furthermore, the greater approval of the aforementioned health claims⁽⁵⁾ has slowly worked its way down the production and product development chain and has seen a slow evolution of products developed that have seen an upswing in food-related utilisation. Indeed, Strychar⁽¹²⁾ has reported that feed (animal) use of oats had declined from 90 to 70% of global production with the commensurate upswing in food and industrial utilisation.

It is clear from the figures that there are favoured regions for growth for many crops, and oats are no exception. Oats tend to be grown in temperate regions (Fig. 3) with reasonably high

rainfall levels and generally in areas that have moderate temperatures: mid to north Europe, the Russian Federation, the USA and Canada comprise the major production regions (Fig. 4 and Table 2 with references therein). Optimum growth conditions are conditions of moderate temperature and long day length. In general, they can tolerate wet weather and acidic soils more effectively than other cereals such as wheat. In addition, and again in comparison with other food cereals, they are relatively resistant to foliar diseases, while requiring comparatively fewer pesticide and fertiliser inputs⁽¹³⁾.

With respect to nutritive and health-beneficial values, there has been a significant level of study into the key factors that affect diversity and content. In essence, there are several drivers for this: cultivars (genetic diversity); soil; climate; agronomy. Changes in nutritive and health-beneficial values as a different cultivar (a cultivated variety of a plant that has been created or selected intentionally and maintained through cultivation) is assessed are well established. A study carried out by Doehlert *et al.*⁽¹⁴⁾ of twelve oat varieties showed that,

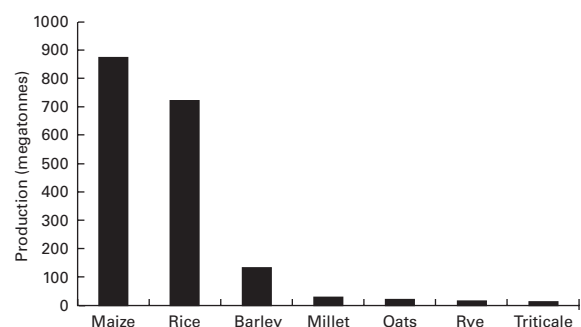


Fig. 1. Global production levels of the main cereal crops (values are for the 2010 production figures)⁽¹⁰⁾.

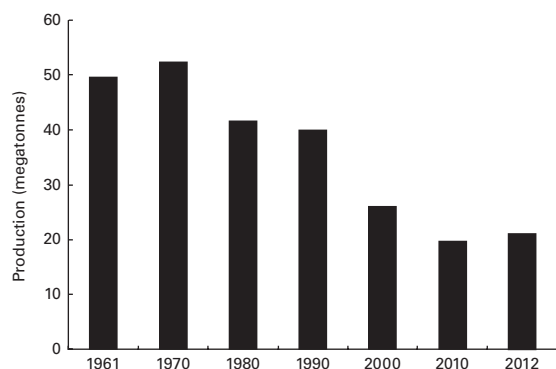


Fig. 2. Global production of oats from 1961 to 2010⁽¹⁰⁾.

even within this limited sample set of cultivated germplasm, the variation in grain yield and starch, oil, protein and β -glucan contents was significant at 31, 6, 34, 56 and 33%, respectively. Other studies^(15–27) have focused more on specific components.

Leonova *et al.*⁽¹⁵⁾ focused on oil content and diversity and reported that, although wild (uncultivated) oat species exhibited higher total oil (% dry seed weight) and 18:1 fatty acid contents, the levels of the beneficial PUFA 18:2 (linoleic acid) and 18:3 (linolenic acid) were enhanced (as a % of the total lipids) in cultivated oats. This corroborates the finding of other similar and limited studies^(16,17). More recently, a more extensive study⁽¹⁷⁾ using 917 oat accessions, mainly representing *A. sativa* but also including other *Avena* species (122 accessions) and cultivated oat replicated at different environments, has also confirmed the elevated levels of linoleic and α -linolenic acids in the cultivated lines. Furthermore, this study found that environment significantly affected only total oil content and not the composition, which is in contrast to the findings of others^(19–21), who reported significant variation in composition. It is worth noting that in these latter studies the geographical variation was much broader than that utilised by Dhanda⁽¹⁸⁾.

The impact of oat genetic diversity is also evident for the health-beneficial component β -glucan, which is currently the main impetus behind much of the breeding effort in oats for human consumption. Several studies^(22–26) have been undertaken in this respect and have identified that the existing range of β -glucan content generally falls within 2.5–8.3% (dry grain). In addition to total β -glucan content, there is increasing interest in β -glucan polydispersity, essentially the relative distribution of polymer molar masses and degrees of polymerisation, with research pointing to biological efficacy and benefits deriving from the higher-molecular-weight components. In fact, molecular weight polydispersity is significant and has been reported to cover the range 65–3100 kDa⁽²⁷⁾.

The environment and agronomic systems can have significant effects on the nutritive and health-beneficial values of oats, and abiotic (non-biological) stress factors, such as temperature, drought/flooding and fertilisation, have been assessed for their impact (Table 2). In general, these stressors are combined under 'environment', despite fertilisation being an agronomic process, and the impact is assessed as such.

For example, Doeblert *et al.*⁽¹⁴⁾ reported that oat yield and starch content were strongly influenced by environment, whereas protein and β -glucan contents were equally susceptible to genetic and environmental influence. Interestingly, Andersson & Börjesdotter⁽²⁸⁾ reported a greater effect of environment on the molecular weight of β -glucan (71%) than on its content (42%). It is worth stressing that these environmental effects do translate through to specific and quantifiable nutritional consequences. A study carried out by Dickin *et al.*⁽²⁹⁾ on the impact of genotype, environment and agronomic management on β -glucan in naked barley grain (a sister species with appreciable β -glucan contents) highlighted that all these factors affected β -glucan content. Also, part of this study was a porridge intervention trial employing lines exhibiting variation in β -glucan content (5.8 v. 4.6 g/100 g (dry material)) to highlight the impact of β -glucan content variation on human metabolism. In this trial, the higher- β -glucan porridge was found to significantly reduce the total glucose released as well as blunt the peak glucose, a phenomenon associated with oxidative stress, inflammation responses and degenerative diseases such as endothelial dysfunction⁽³⁰⁾.

A study carried out in Russia utilising a range of varieties from Germany, the USA, Russia, Canada, Sweden and other countries highlighted some broad environmental effects with oat yields being identified as susceptible to high temperature and drought⁽³¹⁾. Interestingly, Frey⁽³²⁾ reported that the modern oat varieties were more tolerant to drought stress than older ones. Most studies on environmental effects on oats have targeted specific (β -glucan, oil and protein) or gross (yield, lodging disease resistance) components. As has been mentioned above, β -glucan content and polydispersity have been shown to be environmentally influenced, and such studies have been extended to other beneficial components (Table 2). Unsurprisingly, protein content is responsive to fertiliser N addition, with total protein content being optimised by eliminating supraoptimal applied N. Interestingly, the nutritive value with respect to protein amino-acid content did differ between naked and husked oats in response to increasing N inputs⁽¹³⁾.

Oat, similar to any other crop, is a host for attack by plant pathogens, and this attack invariably reduces crop yield and affects composition and therefore the accessibility of high-quality oat for human consumption. Of the viral pathogens,

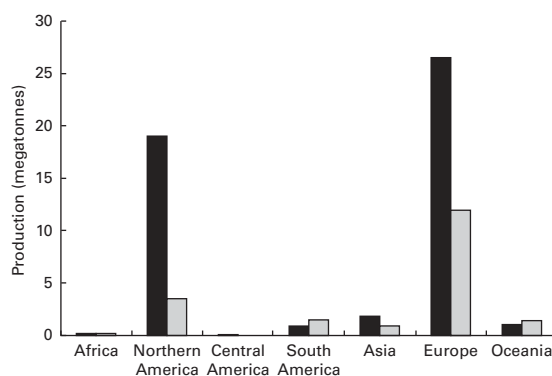


Fig. 3. Regionalised oat production for the years 1961 (■) and 2010 (□)⁽¹⁰⁾.

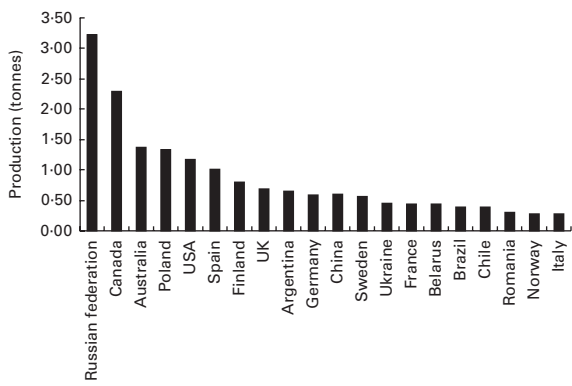


Fig. 4. Top twenty countries for oat production in 2010⁽¹⁰⁾.

barley yellow dwarf virus (also known as red leaf) can cause significant crop and yield losses⁽³²⁾; crown rust⁽³³⁾ (*Puccinia coronata*) and powdery mildew^(34,35) (*Blumeria graminis*) are the prevalent fungal diseases in North America and the cooler, humid regions of Europe, respectively.

However, it is the fungal infection of oats (and cereals) caused by species of the *Fusarium* genus that is of most concern to oat consumption and human health and well-being. These fungi are well reported to produce the mycotoxin trichothecenes, such as deoxynivalenol, nivalenol,

T-2 and HT-2, and some other toxins such as zearalenone and fumonisins B₁ and B₂, and the specific production of these toxins depends upon where the oat is grown and hence the localised fungal strain population^(36,37). The trichothecenes T-2 and HT-2 are the ones commonly reported in infected oats; the physiological consequences of consuming these either directly on the oat (products) or via animals fed with spoiled oat feed are acute, with chronic toxicity potentially leading to induced apoptosis in the immune system and fetal tissues⁽³⁸⁾. A combined approach of targeting resistance in new varieties, particularly using modern genetic/genomic approaches, and adherence to good agricultural practices should see the current-day levels of these deleterious components dramatically reduced.

Oat breeding: cultivars for climate adaptation and pathogen resistance

The production and availability of oats are, as in all crops, affected by agricultural practices and climatic variation⁽³⁹⁾, which in turn may affect plant diseases⁽⁴⁰⁾. If agriculture is to provide sufficient food for a growing population, crops providing a significant complement of the human requirement for nutrition and energy, such as oats, must adapt to climate change⁽⁴¹⁾. These changes will include shifts to mid-latitudes

Table 2. Influence of environment factors on beneficial oat components

Components	Environmental factor	Impact	Reference(s)
β-Glucan – total	Temperature	Generally higher levels in warm, dry climates	Doehlert <i>et al.</i> ⁽¹⁴⁾ , Saastamoinen ⁽⁵⁷⁾ , Anker-Nilssen <i>et al.</i> ⁽⁵⁸⁾
	Precipitation	Moderate rain increased total content. Supraoptimal precipitation yields lower total contents	Doehlert <i>et al.</i> ⁽¹⁴⁾ , Dickin <i>et al.</i> ⁽²⁹⁾ , Brunner & Freed ⁽⁵⁹⁾ , Güler ⁽⁶⁰⁾
	Fertiliser	Total β-glucan is optimised by eliminating supraoptimal applied N	Achleitner <i>et al.</i> ⁽⁵⁰⁾ , Weightman <i>et al.</i> ⁽⁶¹⁾
β-Glucan polydispersity	Temperature	Elevated growing season temperature yields higher-MW β-glucan	Anker-Nilssen <i>et al.</i> ⁽⁵⁸⁾ , Ajithkumar <i>et al.</i> ⁽⁶²⁾
	Precipitation	Reduced the average MW	Andersson & Börjesdotter ⁽²⁸⁾
	Fertiliser	Optimising N increases total β-glucan content, which is correlated with higher-MW β-glucan	Andersson & Börjesdotter ⁽²⁸⁾
Starch	Temperature	Combined as environment – affects starch content, Rapid Visco Analyser™ pasting viscosities, starch swelling volume and differential scanning calorimetry thermal properties	Rhymer <i>et al.</i> ⁽⁶³⁾
	Precipitation		
Protein	Fertiliser	Cultivar-dependent response to N levels: optimising N for yield can reduce starch content	Givens <i>et al.</i> ⁽¹³⁾
	Precipitation	Increasing soil salinity reduced grain protein content. General increase in dry conditions	Kumar <i>et al.</i> ⁽⁶⁴⁾ , Peterson <i>et al.</i> ⁽⁶⁵⁾
	Fertiliser	Total protein is optimised by eliminating supraoptimal applied N. Protein amino-acid compositional response observed between naked and husked oats in response to increasing N inputs	Givens <i>et al.</i> ⁽¹³⁾ , Weightman <i>et al.</i> ⁽⁶¹⁾ , Welch & Leggett ⁽⁶⁶⁾ , Dimitrova-Doneva & Petkova ⁽⁶⁷⁾
Oil	Fertiliser	Generally a reduction in total oil content with increasing added N. Conflicting reports on compositional changes: small but significant increases in palmitic acid (16:0) and linoleic acid (18:2) contents, but decreases in oleic acid (18:1) content with increasing N inputs	Givens <i>et al.</i> ⁽¹³⁾ , Welch & Leggett ⁽⁶⁶⁾ , Dimitrova-Doneva & Petkova ⁽⁶⁷⁾
Phytochemicals	Temperature	Avenanthramides – Content is under environmental influence but poorly defined	Peterson <i>et al.</i> ⁽⁶⁵⁾ , Emmons & Peterson ⁽⁶⁸⁾
	Precipitation		
	Fertiliser	Addition of P sources can increase the levels of the antinutrient phytic acid	Miller & Fulcher ⁽⁸⁾

MW, molecular weight; N, fertiliser nitrogen.

and adaptations to broader temperature ranges, more frequent weather extremes, and longer growing seasons, a shift to sustainable agronomic practices using nutrient-use-efficient varieties (reduced synthetic fertiliser use), greater stress and drought resistance, and elevated dew points. Successful adaptations for oats will require extensive understanding of the molecular mechanisms and pathways involved in, and affected by, abiotic stress factors and sustainable agricultural practices^(39–41). An obvious approach to this understanding includes genetic modelling using tractable plant models such as *Arabidopsis*⁽⁴²⁾ or, more sensibly, an appropriate sister cereal model, such as barley, which has recently had its genome sequenced⁽⁴³⁾. Furthermore, oat, as part of the cereal family, will benefit from the new initiatives such as Modelling European Agriculture with Climate Change for Food Security (<http://www.macsur.eu/>). This knowledge hub gathers the excellence of existing research in livestock, crop and trade science to describe how climate variability and change will affect regional farming systems and food production in Europe in the near and distant future and the associated risks and opportunities for European food security. Such synergistic programmes with modelling on a pan-European scale will invariably benefit future crop-breeding initiatives and effort.

As has been highlighted earlier, powdery mildew, crown and stem rust, and infections caused by species of the *Fusarium* genus are the predominant diseases that affect oats and can reduce crop yield by as much as 50% among susceptible cultivars^(34–37), with, for example, crown and stem rust contributing to significant global reduction in yield and seed quality⁽³²⁾. Barley yellow dwarf disease⁽³³⁾, which has aphids as its primary vector, is considered the most important viral disease of oats, and currently none of the oat cultivars is highly resistant to barley yellow dwarf virus. However, this is a focus in the oat-breeding community, and the identification of cultivars exhibiting degrees of resistance (while maintaining/increasing grain yield) is providing a foundation for further genetic research^(44,45). Germplasm exchanges from specific oat cultivars since the late 1960s indicate a steady improvement in barley yellow dwarf virus tolerance, and this breeding effort has – following multiple collaborative efforts between universities and agriculture centres involving multiple generations of oat genomic clones of global origin, selective crossbreeding and the application of newer genome-mining technologies such as diversity array technology^(46,47) (see below) – produced cultivars that are more resistant to barley yellow dwarf virus and exhibit increased yields.

Oat breeding: state of the art and future plans

Modern-day oat breeding has progressed significantly as a result of the paradigm shift that has occurred in plant biology with the combined advances in molecular biological research, omics technologies, genome sequencing and bioinformatics. Perhaps because oats have (unfairly) been perceived as a relatively unimportant crop, they have not benefited from the level of research that has been put into wheat, rice, barley

and even sorghum – but progress has been made using the approaches mentioned above. Our understanding of oats *per se* and also our knowledge of the rate at which yield, disease resistance, and compositional content and diversity are being manipulated have increased significantly^(44–47). MacKey⁽⁴⁸⁾, for example, highlighted that the yield potential of Swedish oat had remained virtually unchanged over the period from 1910 to 1960, whereupon it increased, with accompanying research effort yielding major increases in harvest index (the weight of a harvested product as a percentage of the total plant weight of a crop) and lodging resistance. This approach became the norm and, as the utility, nutritive value and health benefits (predominantly those attributable to β -glucan) became established, it became imperative that breeding needed to be able to manipulate, and ideally enhance, many of these traits simultaneously. Diverse germplasm has traditionally been used to modulate oat gross (e.g. yield) and specific (β -glucan) parameters. However, modern genetic analytical approaches such as simple sequence repeats⁽⁴⁹⁾, amplified fragment length polymorphisms⁽⁵⁰⁾, restriction fragment length polymorphism⁽⁴⁴⁾ and diversity array technology⁽⁴⁶⁾ are being applied to oat *per se* either in isolation or in unison⁽⁴⁷⁾ to maximise the identification of genetic diversity.

Overall, these approaches identified that, due to the limited initial selection of landraces (essentially traditional localised varieties), diversity has become limited and that if there are to be significant increases in, for example, the levels of β -glucan and vitamins, reassessment and integration (introgression) of the wild material into breeding programmes are necessary. Such an approach is already being undertaken on a significant scale for sister grass species *Lolium perenne* (perennial ryegrass), with the introgression of the entire genome of *Festuca pratensis* (meadow fescue) into *L. perenne* in overlapping chromosomal segments with the aim of crop improvement by tapping the *F. pratensis* untapped reservoir of genetic variation for a wide range of agronomically important traits⁽⁵¹⁾. This approach, using a combination of modern genetic/genomic and high-throughput analytical approaches, makes this an achievable goal and one that can deliver on the development of oat for food uses as well as targeted utilisation in other sectors, such as cosmetics and food ingredients⁽⁵²⁾.

Modern commercial oat breeding is a complex and structured system that combines the selection and assessment of the breeding material and progeny, normally at a restricted acreage level, with the commercial trialling over broader and diverse environments (Fig. 5). As with other crops, this is a rolling-and-staggered approach to ensure the continuous production of better and distinct varieties that match the current and projected market requirements. It is clear that going forward there will be multiple targets for oat breeding to address^(26,53). From the aspect of new product development, these targets will undoubtedly include the following:

- (1) Oat β -glucan – building on the approved health claim.
- (2) Nutritional components – good source of protein and unsaturated fatty acids.

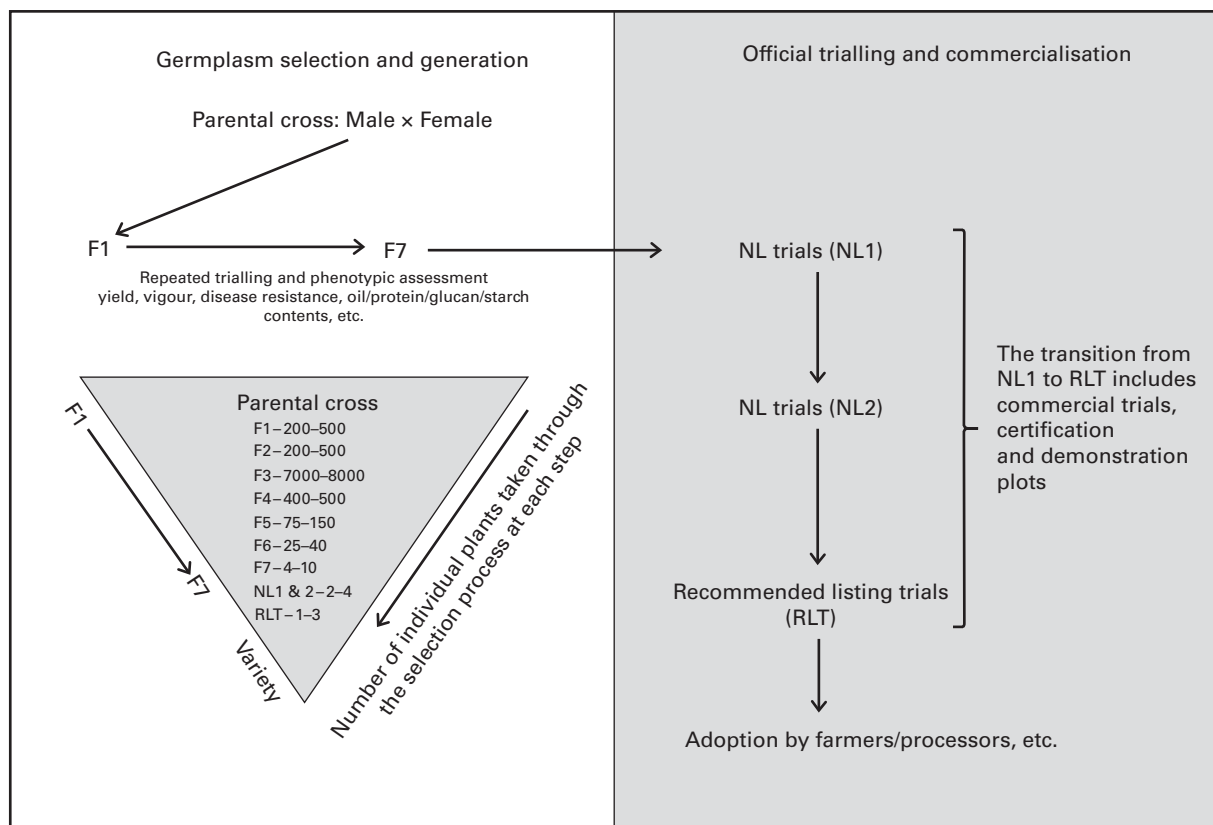


Fig. 5. A schematic description of the UK process of oat variety generation with approximations of the scale of effort involved. The parental cross schematic highlights the scale of plant lines needed to progress from the initial parental cross through generation to be multiplied up for assessment and ultimately for recommendation (RL) to farmers. NL (National Listing): this is a legal requirement for new varieties of the main agricultural and vegetable species that seeks to ensure that no new variety is marketed unless it is genuinely new and, for agricultural crops, an improvement in key characteristics on varieties already being sold. RL (Recommended Listing): this provides information on yield and quality performance, agronomic features and market options for recommended varieties to assist growers with variety selection. Varieties are generally trialled on an annual basis while they remain on the Recommended List. For oats in the UK, this is administered by the Home Grown Cereal Authority. RLT, Recommended Listing trials.

- (3) Desirable organoleptic properties – these are predominantly derived from the action of processing/cooking on the oat lipid content and vary with process/cooking conditions and lipid composition.

What does the future hold?

The advances now being made in oat biology as a consequence of technological advancements in other cereals, such as rice, wheat and barley, are exponential. The adoption of genotype by sequencing⁽⁵⁴⁾ holds major potential for identifying both the variation in and the genes underpinning the desirable nutritional and health-beneficial traits, meaning that these genome regions can then be used as molecular markers to accelerate trait enhancement in future germplasm. Furthermore, this approach can also be exploited along with transcriptome profiling that uses deep-sequencing technologies⁽⁵⁵⁾ to tease out the genetic drivers to the environmental response that we have already shown (Table 2) can impinge upon nutritional and health-beneficial contents. Alignment of this with high-throughput and detailed phenotyping systems,

such as metabolomics, will ultimately lead to an accelerated development of new and tailored oat varieties.

The next step in the development of oats will be the elucidation of the genome sequence, and this is being actively pursued by a consortium of oat scientists across the world.

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