agronomy

Review

Domestication of Perennial Flax Using an Ideotype Approach for Oilseed, Cut Flower, and Garden Performance

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Abstract: Flaxseed (*Linum usitatissimum*) has recently grown in popularity as a health food due to its high levels of omega-3 fatty acids. Many undomesticated *Linum* species possess a similar oil profile, in addition to perenniality, and could, therefore, provide similar products in addition to ecosystem services such as soil retention, improvements in water quality, and pollinator services. Many *Linum* species also possess ornamental qualities, e.g., blue flowers, which could provide added value as a new cut flower crop or garden herbaceous perennial. A perennial flax breeding program will be initiated by screening of *Linum* accessions for key agronomic and horticultural traits. Herein, we outline an ideotype approach which will enable identification of top herbaceous perennial candidates for domestication based on qualities relevant to oilseed, cut flower, and garden herbaceous perennial crop uses. In this review, we summarize the concept of ideotype breeding as it relates to perennial crop domestication and outline considerations for ideotype design. The tools outlined herein should prove useful to other breeders and especially for undomesticated crops. Whether the ideotype concept is applied as a framework for selection or simply as a means of generating hypotheses, applying this approach can provide structure to breeding programs with complex objectives.

Keywords: ideotype; crop domestication; perennial grains; floriculture; plant breeding; *Linum*; ecosystem services

1. Introduction

The term "ideotype," literally meaning 'a form denoting an idea,' was first coined by Donald (1968), who described it as "a biological model which is expected to perform or behave in a predictable manner within a defined environment" [1]. This was the first time that the application of plant models to breeding had been systematically outlined. Jennings was the intellectual inspiration for Donald's paper, with Jennings having earlier defined a rice "plant type" which would integrate multiple traits to boost yield, based on contemporary knowledge of plant physiology [2]. At the time, Jennings was looking for ways to close the yield gap between developing nations located in the center of the origin of rice and developed nations, the latter of which regularly achieved much higher yields [2]. By contrast, Donald's ideotype breeding approach was intended to break yield barriers and eventually supplant traditional breeding methods for well-studied row crops such as wheat, which he himself worked on. In concluding his paper, Donald optimistically remarked, "eventually most plant breeding may be based on ideotypes" [1].

While Donald's predictions have failed to materialize, the concept of the ideotype model has nevertheless persisted. Breeding programs with diverse goals or those that work with plant material which requires multi-faceted improvements have benefited from the ideotype concept. The most detailed and successful example of ideotype-based breeding is from research conducted at the International Rice Research Institute (IRRI) in the Philippines. This has already been detailed extensively in reviews [3,4], although we will later discuss some of the lessons from this program. The ideotype concept has also been used extensively as a framework for crop simulation modeling [4–7]. Other examples of implementing ideotypes come from studies in forestry [8] and in reducing the invasiveness potential of ornamental horticultural crops [9].

One of the greatest untapped opportunities for ideotype breeding exists for breeding undomesticated perennial crops due to the sheer number of traits that require improvement [10]. Most domesticated crop plants have several traits in common, including increased grain/fruit size, reduced branching, gigantism, non-shattering, loss of seed dormancy, synchronous maturation, and loss of toxic compounds. These traits are commonly referred to as the "domestication syndrome," as they are changes that took place during domestication to make the crop more agronomically productive and useful to humans [11]. For a perennial grain to successfully integrate into our current agricultural system, it will need to possess most, if not all, of these traits.

Perennial crops also require unique survival structures not typically found in annual crops. In the Midwestern United States, for example, perennial grain crops must produce vegetative structures capable of overwintering, unlike annual crops which are regenerated entirely through seed [12]. While a lengthened growing season allows perennials to achieve greater light and nutrient capture relative to their annual counterparts, these winter survival needs may still limit yield potential [12,13]. It is not yet clear how this additional factor will change the overall physiology and management of perennial grain crops.

2. Traditional Versus Ideotype Approaches to Breeding

Donald defined two primary approaches to traditional breeding, namely "defect elimination" and "selection for yield", the latter being the most common practice in plant breeding [1]. Selection for yield generally does not take other traits into account, although they may be linked. The process involves hybridization of elite parents to generate segregating populations. Out of these populations, high yielding material is further selected and the process repeats again. With this method, the breeder is less likely to understand what enabled the increase in yield to occur or which non-target traits might be changing in response to selection for yield [1]. Defect elimination complements selection for yield by removing traits which are known to severely limit yield gains, such as a susceptibility to lodging or disease. While these methods have resulted in yield gains over time, they do a poor job integrating knowledge of crop physiology [1]. These traditional methods of breeding often prove inadequate for more complex breeding scenarios such as crop domestication, wide adaptation of selections, or the improvement of ornamental crops [9].

In contrast to traditional methods of breeding, Donald's ideotype utilizes a whole-system modeling approach. To begin building an ideotype model, one must first define traits of interest based on the goals of the program, as well as prior knowledge of the crop biology, physiology, discipline-specific production requirements, and other relevant fields. Then, for each of these traits, an ideal phenotype is defined. For example, one of the driving factors behind Donald's original wheat ideotype is that it would minimize the competition between plants in a crop community. The trait phenotypes outlined in this model were chosen based on contemporary knowledge of crop physiology, as well as ease of measurement [1]. Note how this approach considers questions of agronomic performance upfront before any selection is made, something which typically does not occur until conducting yield trials under a traditional breeding protocol. If used correctly, the ideotype approach helps to prioritize multiple unrelated traits, as well as generate testable hypotheses about how changes in one trait could affect the overall performance of the plant or crop community [1,14].

The true utility of an ideotype approach derives from the iterative nature of its model-building and goal setting (Figure 1), which is what most distinguishes ideotype breeding from traditional methods [14].

From the outset, devising an ideotype model gives the breeder a clear picture of their overall goals, as well as the limits of their knowledge about the cropping system. The hypotheses generated through this process are then used to improve knowledge of the system and refine the current model, leading, in theory, to more effective selection over time. The ideotype model also exists as a framework for understanding current research needs and the resources necessary to pursue them [14]. It exists as a central organizing principle around which knowledge from multiple fields of study (i.e., genetics, physiology, or agronomy, etc.) can be discussed and integrated with overall project goals.

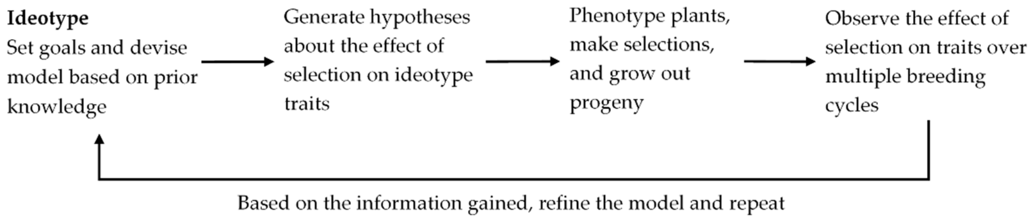

Figure 1. The reiterative ideotype approach of designing and adjusting a crop ideotype model.

A common misconception about ideotype breeding is that it exists in opposition to traditional methods of breeding and selection. Instead, ideotype models should be thought of as a complement to, not a replacement for, traditional breeding methods [3,14]. As discussed, the ideotype model should never be static but should change as more knowledge is gained about the particular trait or system. Deficit elimination can be a very important part of ideotype breeding and selection for yield almost inevitably becomes a factor, such as in the case of Peng et al. [3], where ideotype goals were achieved first, followed by selection for yield in order to generate suitable cultivars. Donald himself argued that "rigorous selection for yield" would likely be necessary for any cultivars produced according to the model approach [1].

It is important to remember that the ideotype, selection for yield, and defect elimination strategies can and should be used interchangeably, depending on the current breeding objective(s). For example, a modern maize breeding program may predominantly pursue selection for yield. However, if a novel disease resistance trait is identified, that program may spend a few years practicing defect elimination in the inbred lines to remove any disease susceptibility. For most maize breeding programs, ideotype breeding may never be completely useful because most major domestication traits are already fixed [15]. By contrast, a breeder working to develop perennial maize would probably want to take an ideotype approach at times in order to help prioritize the many challenges involved in achieving that goal [16,17].

Donald specifically identified cereals as being the most suitable cropping system for the ideotype approach due to the level of available knowledge about their physiology relative to other crops [1]. However, the ideotype method has found limited adoption among cereal, row crop, and ornamental breeders. One exception in ornamental breeding has been with the garden chrysanthemum, which has seen a series of ideotypes developed [18,19], starting with the initial design proposed by Langton, 1976 [20]. In row crops, the lack of adoption is probably because traditional breeding methods for row crops quickly outpace ideotype programs in terms of yield gains, so few ideotype programs ever persist long enough to determine whether the new traits can be effectively integrated into high-yielding lines or whether there is any advantage to integrating ideotype traits into existing germplasm in the first place. While the ideotype method will surely continue to be explored in annual cropping systems, we believe that the greatest potential for the technique lies in the domestication of new species, particularly as perennial crops [10,21]. Undomesticated species have the most to gain from the ideotype approach due to a lack of prior knowledge about the cropping system or preferred breeding methods.

3. Limits of the Ideotype Approach

As with all plant breeding techniques, there are limits to the ideotype approach. Many of these constraints are biological in nature, while others are logistical. One of the most important biological constraints to account for is the possibility of negative correlation between traits. In other words, selecting for a trait of interest might cause unintended and undesirable effects on other linked traits. For example, in wheat the number of grains per ear is negatively correlated with the total number of ears [1]. Similarly, rice panicle size is negatively correlated with panicle number/m^2 [3]. A more difficult example could arise from correlation of an important yield component trait with severe disease susceptibility. Any two traits could be negatively correlated due to close proximity in the genome or because of some physiological constraint; it is generally impossible to anticipate these negative correlations until selection occurs. While negative trait correlations are an issue regardless of approach, they can have a large impact on the ideotype model once discovered.

Pleiotropy is another biological constraint on ideotype breeding. When seemingly unrelated traits share a physiological pathway, a change to one of these traits may have large effects on the others. Again, this is hard to predict until selection takes place. An example of unanticipated pleiotropic effects is the case of the 'multiple awns' trait in barley, which was shown to increase photosynthesis, but always led to a decline in yield after introgression into elite lines [14]. A similar phenomenon can occur during selection which is called trait compensation. In this case, the anticipated effects of modifying one trait are cancelled out by an opposite compensatory effect in another trait. For example, in barley, it was thought that decreasing stomatal density would decrease leaf conductance, and therefore result in better drought tolerance. Instead, decreased stomatal density was associated with an increased stomatal size, which compensated to maintain the same level of leaf conductance overall [22].

A final biological consideration is that crossing elite lines with inferior donor germplasm can cause severe linkage drag when attempting to combine favorable traits. This can require multiple cycles of breeding in order to recover the overall yield or quality of the line to previous levels [14]. Overall, these biological considerations solidify the notion that an ideotype cannot remain a static model (Figure 1). Discovery of some unfavorable genetic effects could require significant rearrangement of goals, priorities, or the entire ideotype model itself.

There are also several logistical challenges involved with ideotype breeding that should be considered prior to adoption of this strategy. First, one must account for the fact that stacking multiple traits will require many cycles of breeding and/or large population sizes. There is also the inherent risk that the initial ideotype may completely fail to achieve goals if the model assumptions are proven false. Unlike selection for yield per se, which works at some level regardless of the specific cropping system, misguided ideotype model assumptions may cause selection to move in the wrong direction relative to project goals. In such cases, the ideotype must be adjusted and the program started essentially from scratch.

As we have already discussed, it is also difficult for ideotype models to compete with breeders using traditional methods in domesticated species, at least from the outset. However, because perennial crop domestication is a long-term endeavor, by default, investment in maximizing understanding of the system and effective breeding methods is more likely to pay off. There is also less pressure from competitors working in crop domestication, since the initial capital costs and length of time to reach a viable product are too high for most private sector breeding programs.

Finally, one should consider the cost of phenotyping when using an ideotype approach. Ideotype breeding typically requires a greater number and variety of traits to be measured each breeding cycle. By contrast, traditional methods typically only measure yield, yield component traits, and a few other major factors like disease or pest resistance. The amount of knowledge gained through ideotype breeding is maximized if the same traits are measured year after year, so that changes in response to selection can be tracked across the whole organism. Unfortunately, the cost of phenotyping is often high, so the breeder must carefully choose which traits are worth measuring year after year. Nonetheless, given the recent technological innovations, e.g., use of drones, that have streamlined phenotyping, it may be easier to amass big data sets for this purpose [23]. One way to gather more information about which traits are useful is to do a detailed initial screening, which is the first step we propose for applying the ideotype approach to perennial flax domestication. Additionally, the reduced cost of next-generation sequencing has created an opportunity to use genomic selection models for traits which are difficult to measure. The applications of genomics towards the acceleration of crop domestication have undergone detailed review elsewhere, e.g., in [21,24,25], and in time we intend to also develop these tools for the breeding of perennial flax.

4. Principles of Successful Ideotype Breeding

(1) Rely on the method of "hypothesis and test" to refine ideotypes [1]
(2) Define what is known about the system, including the environment and the crop itself [14]
(3) Choose goals which are realistic given existing trait values and the level of diversity present in the germplasm [3,14]
(4) Begin with as large and diverse of a germplasm pool as possible [9,14]
(5) Integrate knowledge from multiple disciplines when adjusting model characteristics [4,6,26]
(6) Identify traits that are easily scored but which correlate with a desired outcome [7,14]

5. Perennial Flax Domestication

The University of Minnesota (UMN) was once very active in breeding annual flax (*Linum usitatissimum*), but the program was terminated in 1984 after the last Minnesota Agricultural Experiment Station (MAES) flax breeder retired [27,28]. However, flax has received increased attention lately due to its high levels of ω-3 fatty acids, which have been associated with decreases in cardiovascular disease, hypertension, atherosclerosis, diabetes, cancer, arthritis, osteoporosis, autoimmune, and neurological disorders when included in the diet [29–31]. Flax also has many secondary uses, such as in the manufacture of linoleum, linen cloth, fine paper, paints, varnishes, and animal food and bedding products [27–29,32,33]. These trends toward "green" flax-derived products may partly explain increases in global flaxseed production between 2007–2017, from 1.66 million tonnes to 2.97 million tonnes [28,34]. Despite these increases in global production, the United States saw a decrease in total production from 2007–2017 [34].

In response to this increased demand for flaxseed, the UMN is investigating the feasibility of perennial flax improvement for agronomic and horticultural applications. Most wild species of flax have high levels of ω-3 fatty acids, similarly to *L. usitatissimum*, making them a suitable alternative for the health foods market [35,36]. *Linum* species also possess a range of desirable ornamental traits, but have undergone little formal improvement as a horticultural crop [36–38]. Blue flowered species like *L. perenne* and *L. lewisii* can often be found in pollinator mixes and have potential for added value as a new cut flower crop [39,40].

Efforts to domesticate perennial flax are being conducted as part of the Forever Green Initiative (FGI), a research group at the UMN with the goal of encouraging year-round cover on the MN agricultural landscape. The FGI is developing crops to counteract negative environmental impacts associated with modern agricultural practices, such as a decline in soil and water quality [41,42]. Best management practices outlined by the Minnesota Pollution Control Agency (MPCA) for reducing nutrient losses from agricultural fields recommend integrating "perennials planted in riparian areas or marginal cropland; extended rotations with perennials" into current agricultural systems as part of the solution to this problem [43]. The FGI, therefore, focuses primarily on winter cover crops and perennial grain species that are winter hardy, provide ecosystem services, and have economic value to the farmer [44].

We model current perennial flax domestication efforts using the pipeline strategy outlined by DeHaan et al. (2016) [45]. One of the first steps in this approach involves noting the relative strengths and weaknesses of each species, genotype, or individual, relative to predefined criteria. This is essentially a modified ideotype breeding approach applied to "domestication syndrome" traits [37]. As domestication progresses, individual plant trait values relative to the ideotype can be used to prioritize selection as well as the overall domestication strategy for that species [45]. This approach is being used to screen perennial flax (*Linum* spp.) germplasm to determine its domestication potential. Ideotypes for various potential applications are outlined in detail in the following sections. These will be used during the initial stages of germplasm evaluation to rank lines based on their performance in each category. The initial selections made during this first phase of domestication will form the foundation of future perennial flax breeding efforts at the UMN. Given the potential long-term investments of time and money into this program, it is essential that the germplasm selected during this phase is of the highest quality possible for the chosen breeding objectives. Additionally, a thorough phenotypic investigation will produce data which is relevant to seed repositories like United States, Department of Agriculture, Germplasm Resources Information Network (USDA-GRIN), Germplasm Resources Information Network, Canada (GRIN-CA), and future researchers who wish to use this material.

6. Perennial Flax Ideotypes

6.1. Agronomic: Oilseed

The proposed oilseed ideotype is based on traits intended to maximize yield, marketability of the seed, and ease of management and breeding (Table 1). Yield per se is also included in this list, as this will be one of the top criteria for selection and may inform future modifications of the proposed ideotype model. However, there are many other traits which are predicted to maximize performance.

Table 1. The proposed perennial flax oilseed ideotype including the ideal phenotypes, their measurement, and rationale for the choice of traits.

Oilseed Ideotype			
Ideal Phenotype	**Measurement**	**Rationale**	**Reference**
Uniform habit	Plant L × W × H (cm)	More effective shading of weeds	[46]
Upright habit	Plant stature rating (1–3)	Enable increased planting density	[47]
Highly branched stems	Technical stem length (figure)	Annual oilseed flax is typically highly branched; supports greater seed production	[38]
Weak stem fibers	Stem diameter (mm)	Ease of mechanical harvest	[48]
Uniform boll height	Variance in technical stem length	Ease of mechanical harvest	[45]
Non-shattering (indehiscent bolls)	Number of seeds per boll Degree of spontaneous capsule opening (Figure)	Reduce yield loss and numbers of volunteer plants; reduced invasiveness	[9]
High yielding	Total seed weight (g)	Economic viability for the farmer	-
Large seeds	One hundred seed weight (g)	Correlated with higher yield and oil content; improved emergence	[38]
Yellow seed coat	Royal Horticultural Society (RHS) color swatches Colorimeter	Provides product differentiation; yellow seed coat required for baking	[28,32]
Oil composition comparable to cultivated flax	Seed samples to external testing lab	Ability to reach functional/health foods markets	[35,36]
Low in antinutritionals	Seed samples to external testing lab	Safe human and animal consumption	[49]
Low heavy metal accumulation	Plant samples to external testing lab	Safe human and animal consumption	[50]
Early maturity	Harvest date	Early maturing cultivars have the potential for two harvests per season	[39]
Homostylous, self-compatible	Flower morph (pin/thrum)	Ease of breeding and developing inbred lines	[51]
Fast germination, high germination rate, seedling vigor	Time to emergence Germination rate Seedling survival	Improved stand establishment	[52]

A compact, upright habit is desired for multiple reasons. This characteristic reduces crowding, allowing for increased planting density and decreased row spacing, which have been shown to result in improved yield in cultivated annual flax (*L. usitatissimum*) [47]. An upright habit prevents contact with the soil, reducing the risk of soil-borne disease and rot. Keeping the five-lobed seed capsules elevated is also important for preventing loss of yield during mechanical harvest. Upright, compact habit will be quantified through length (cm), width (cm) and height (cm) measurements, as well as a rating of plant stature (1–3; prostrate–erect).

The proposed oilseed ideotype integrates multiple stem-related traits, at least during the initial years of surveying. Stem branching habit will be quantified by measuring total stem length (cm) and length from the stem base to the first branch point. These measurements define the technical stem length, or the proportion of the stem with side branching (Figure 2) [38]. In cultivated annual flax (*L. usitatissimum*), oilseed cultivars are typically highly branched relative to fiber types. Therefore, highly branched stems will also be considered the ideal type with which to start. Uniform seed height is also desired, although this trait is difficult to measure directly. It will be approximated by the variance in technical stem length for a given line. High variance for this measurement would suggest a non-uniform seed height throughout the plant. Finally, stem strength will be characterized through a measurement of stem diameter (mm), with thinner, weaker stems being desired for ease of mechanical harvest, although this must be balanced with the ability to resist lodging [48,53].

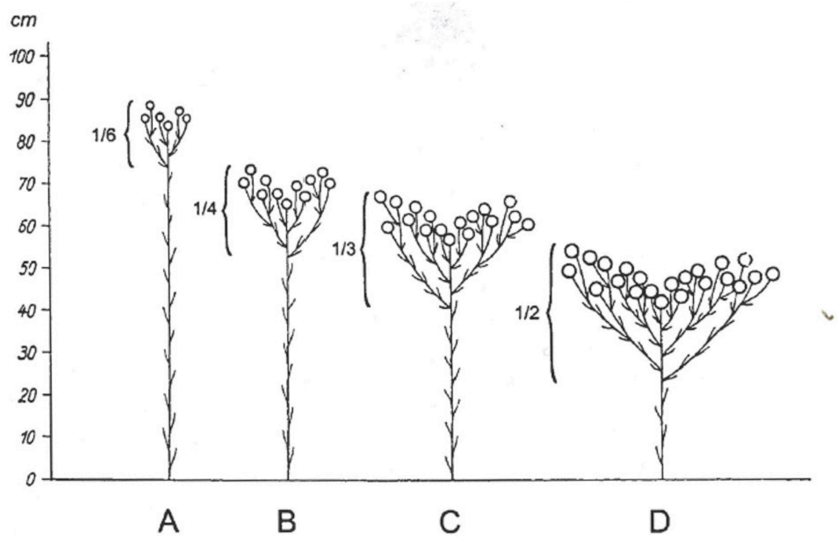

Figure 2. Technical stem length ranges occurring in flax; the part of the stem without side branches defines the technical stem length. The proportion of the stem with branches is indicated. (**A**) Typical fiber flax; (**B**) and (**C**) intermediate flax; and (**D**) large-seeded flax. (Figure and caption adapted from Diederichsen and Richards, (2003)) [38].

Loss of shattering is a classic domestication trait with a large influence on seed yield. Shattering will be rated visually as the degree of spontaneous capsule opening (Figure 3) [38]. Shattering will also be measured post-harvest as the number of seeds per boll, with ideal types possessing greater values for this trait.

Additional seed-related traits of interest are seed size, oil yield and oil composition. Seed size will be measured as the 100 seed weight (g). In cultivated flax (*L. usitatissimum*) large seed size is correlated with higher yield, oil content, and better emergence [38]. Oil yield and composition will be determined by sending samples to an external testing lab. The oil profile must be similar to cultivated flax (*L. usitatissimum*) and be free of antinutritional compounds in order to target the same health food markets [49,50]. A yellow seed coat color is also desired for applications in baking (Figure 4) [28,32]. After harvest, seed color will be measured using a handheld colorimeter [54] and/or Royal Horticultural Society (RHS) color chart [55].

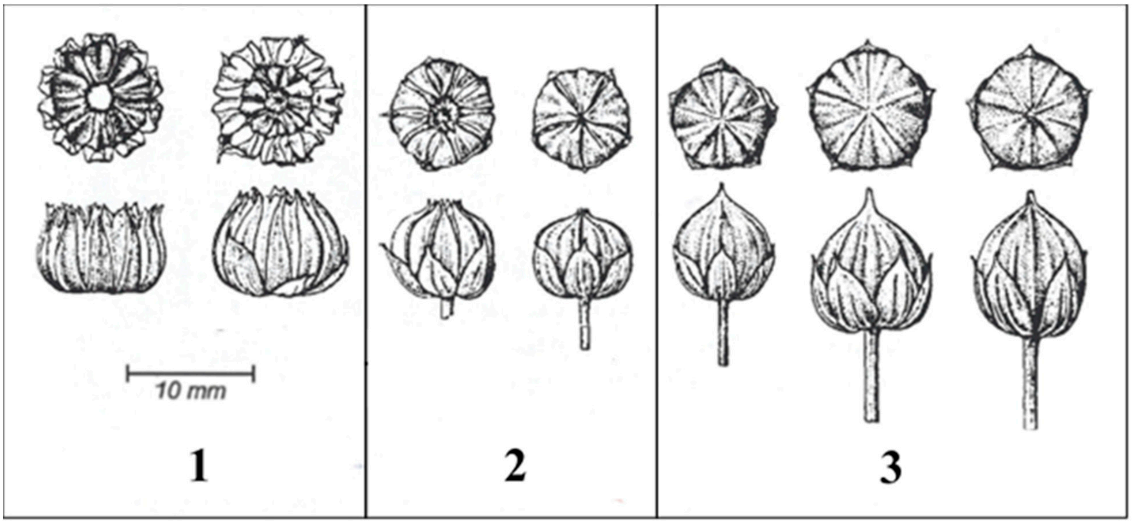

Figure 3. Degrees of spontaneous opening in mature flax capsules. Rating scale: (**1**) strongly dehiscent, seed shatters freely; (**2**) slightly dehiscent, minimal seed shattering; and (**3**) indehiscent, no shattering (adapted from Diederichsen and Richards, (2003)) [38].

Figure 4. Variation in seed coat color observed in annual flax (*L. usitatissimum*). Lighter seed coats are desired for their aesthetic appeal [28,32] (figure adapted from Diederichsen and Richards, (2003)) [38].

The ideal cultivar should have fast and consistent germination, as well as good seedling vigor. These will be measured by tracking germination rate and seedling survival in a greenhouse. Early germination will be screened by tracking germination week. Maturity and harvest date will also be recorded in the field. Early maturing cultivars are preferred, as these could potentially yield two harvests per season.

Finally, the ideal mating system is homostyly and self-compatibility to produce a perennial flax cultivar. Heterostyly is a self-incompatibility system found in many species of *Linum*, in which two flower morphs, termed pin and thrum, prevent selfing [51]. A homostylous, self-compatible species is preferred as it would enable inbred lines to be developed quickly, greatly simplifying the process of breeding.

6.2. Horticultural: Cut Flower

The proposed cut flower ideotype is intended to maximize the quality and value of the stems for floral design applications (Table 2). As with the oilseed ideotype, an upright habit is desired to keep flowering stems off the ground in order to preserve their quality. However, unlike the oilseed ideotype, cut flower cultivars should have long, unbranched stems. This will be determined by the technical stem length (Figure 2) [38].

Table 2. The proposed perennial flax cut flower ideotype with the ideal phenotypic traits, the measurements required to quantify them, and the rationale for the choice of each trait.

Cut Flower Ideotype			
Ideal Phenotype	**Measurement**	**Rationale**	**Reference**
Upright habit	Plant stature rating (1–3)	Keeping flowering stems off ground preserves quality	-
Long unbranched stems	Technical stem length (figure)	Increased value for floral design due to greater range of uses	[38]
Long vase life	Vase life experiments	Greater flexibility of uses as a cut flower	[56]
Flower longevity ↑	Vase life experiments, field observations	Flax petals often drop hours after opening but it may be possible to select on existing variation for flower longevity	[57]
Large flowers	Flower diameter (mm)	Ornamental quality (flower power)	[57]
>50% petal overlap	Flower shape (figure)	Ornamental quality (flower power)	[57]
Vibrant color	RHS color swatches	Ornamental quality (flower power)	[57]

Vase life will be measured in a separate experiment, the methods for which are outlined by Tork et al. (2019) [56]. A long vase life is desired as this provides greater flexibility of use in floral arrangements. Individual flower longevity is also desired and will be tracked during the vase life experiment.

The final component of the cut flower ideotype is large, vibrantly colored flowers with nearly continuous petal overlap. To determine flower size, flower diameter (mm) will be measured when flowers are fully open. Following measurement, flower color will be characterized using an RHS color chart [55]. Petal overlap will then be characterized using a rating of flower shape (Figure 5) [38]. In this scale, flowers are grouped based on shape ((A) tube, (B) funnel, and (C) bowl) and petal overlap ((1) petal overlap >50% and (2) petal overlap <50%). The desired phenotype would have a rating of 1C using this scale.

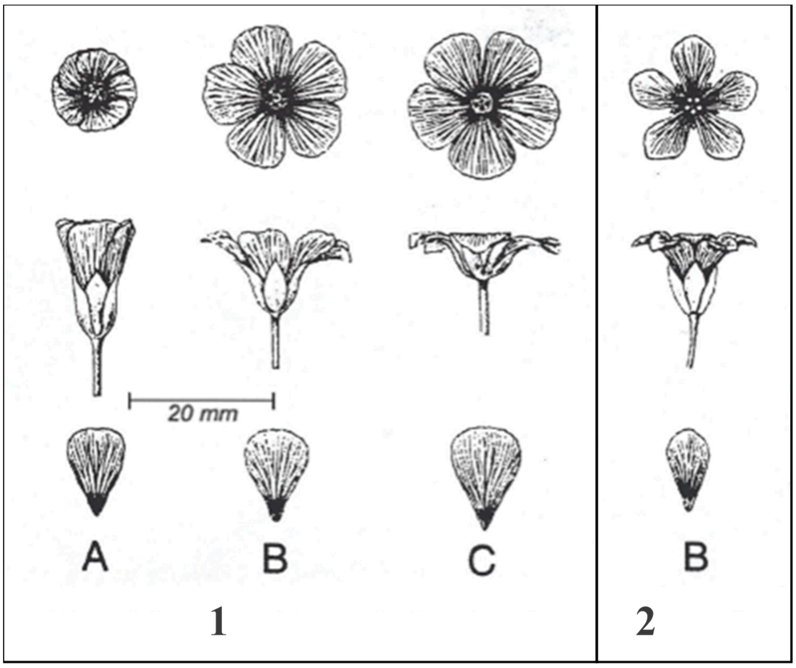

Figure 5. Shape of flowers in flax: (**A**) tube, (**B**) funnel, and (**C**) bowl; (**1**) petals overlap more than 50% and (**2**) petals overlap less than 50% (figure and scale adapted from Diederichsen and Richards, (2003)) [38].

6.3. Horticultural: Garden Ideotype

The proposed garden bedding plant or herbaceous perennial ideotype is based on traits which provide ornamental quality, consumer appeal, and pollinator services (Table 3). Like the cut flower ideotype, large, vibrantly colored flowers with nearly continuous petal overlap are desired (Figure 5).

Table 3. The proposed perennial flax garden ideotype with the ideal phenotypes for various traits, the measurements required to quantify them, and the rationale for the choice of each trait.

Garden Ideotype			
Ideal Phenotype	**Measurement**	**Rationale**	**Reference**
Uniform habit	Plant L × W × H (cm)	Consumer preference for uniform habit and compact forms.	[58]
Long flowering period	Weekly flowering notes	Ornamental quality (flower power) and pollinator services	[58]
Large flowers	Flower diameter (mm)	Ornamental quality (flower power)	[58]
Vibrant color	RHS color swatches	Ornamental quality (flower power)	[58]
>50% petal overlap	Flower shape (figure)	Ornamental quality (flower power)	[58]
Unique characteristics	Field observation	Able to be differentiated from other cultivars on the market	[58]
Pollinator friendly	Pollinator visitation, nectar production	Critical ecosystem service with potential for added value as a result of consumer appeal	[59]

In addition, a long flowering period would extend peak ornamental quality and increase the pollinator services provided by the plant. The number of days in flower will be determined from weekly flowering notes taken in the field.

The ornamental horticultural industry generally prefers small, compact forms of landscape plants with various plant habit types (spherical or mound, upright, or groundcover), which increase profits for the grower since production is more efficient and shipping easier [60]. This trait will be characterized by length (cm), width (cm), and height (cm) measurements in the field for translation into bedding and herbaceous perennial plant production to achieve the targeted plant size within the acceptable aesthetic ratio in containers (plant height = 1.5× to 2× container width or height, whichever is greater).

The final component of the garden bedding plant ideotype involves unique characteristics which would differentiate the plant from other cultivars or series on the market. This could include a unique flower shape, pattern, or plant growth habit. Future work should also investigate pollinator visitation and nectar production as a means of breeding for pollinator services.

6.4. Potential Future Ideotypes

Additional potential ideotypes could focus on improving ecosystem services outcomes. For example, breeding for improved pollinator services could entail selecting plants for which there is increased visitation or an increased diversity of pollinators. Other traits could include increased nectar production and flower colors or patterns which are attractive to pollinators. Flax has also been used in remediation of contaminated sites as it is an effective accumulator of heavy metals [50]. An additional ideotype could focus on traits like rate or capacity of heavy metal accumulation and ability to thrive in disturbed sites with contaminated soil. Ability to uptake excess nutrients from buffer regions of waterways is an additional means of improving perennial flax ecosystem services which could provide value to the general public. Part of the consumer appeal of perennial crops is that they are able to provide these unique ecosystem and pollinator services. Increasing the effectiveness of these services could therefore be an added source of value for perennial flax. Traits such as non-shattering seed pods could also be introgressed into ornamental type plants to reduce their potential for invasiveness [9].

Historically, flax has had great economic importance as a fiber crop, although in modern times linen has been largely replaced by cotton and synthetic fibers [27,29]. However, it may be possible to generate increased demand for linen by marketing desireable properties such as strength, wicking ability, and that it is fully hypoallergenic and biodegradable [29,61]. Although selection for fiber production is not being explicitly pursued, selecting for increased stem length in cut flower lines should lead to adapted populations which possess many of the desired traits for fiber production. Collaborations with materials scientists will need to be initiated prior to formal development and testing of ideotypes for fiber and dual-purpose fiber/oilseed types. Establishing suitable markets for perennial flax fiber is expected to be more challenging compared to oilseed and ornamental types, which can leverage existing supply chains in the seed processing and greenhouse production industries, respectively.

Breeding for ecosystem services and fiber production both have unique challenges that will require greater organization and investment to address. Pursuing ecosystem services goals will require collaborations with experts in entomology, soil science, hydrology, and agroecology, etc., while breeding for perennial fiber flax will require the the intersection of breeding, materials science, and marketing. Despite these added complexities, it is likely that fiber and ecosystem services objectives will be pursued in the future as added sources of value for the program.

7. Discussion on Methods of Selection

One critique of ideotype breeding mentioned in Donald (1968) is that the model approach introduces bias from the breeder about what is considered 'good' without allowing the highest performing lines to emerge naturally. He mentions an additional critique which states "only if we breed and test many different models, or a series of models . . . , can we determine the advantage, if any, of the preferred model" [1]. Donald did not elaborate on this critique in his original paper, but it seems surprising that this would be framed as a barrier to the ideotype approach. For perennial crop domestication, we consider testing multiple models a necessary step in finding the most effective long-term approach. A similar sentiment was expressed by Rasmusson (1991) who stated that "Postulating a single ideotype for a given crop is too confining" [14]. Each variation of the model should be approached without much expectation of the results. It is more important that clear decisions are made about what is selected for, followed by careful observation of the resulting populations and effective documentation, so that the breeding program maintains continuity regardless of employee turnover.

We find no major reason, apart from space and time constraints, that selections cannot be made in multiple directions, at least initially, in order to determine which models have the most success. Selection for yield per se can also occur at a limited level so that the effect on non-target traits from this 'traditional' approach can be compared to the various ideotypes. As time goes on, and the most effective methods emerge, the program can narrow its focus and begin to drive domestication strongly in one direction or another. Depending on whether agronomic or horticultural goals (or both) end up generating the most value for the program, resources can be divided accordingly. This, we think, should be a much more effective method for improving and understanding a new crop compared to championing a single model, as is suggested by Donald (1968) [1]. An additional advantage to using a multi-ideotype approach is that greater genetic diversity will be maintained as domestication progresses [14,21,25]. Even if one set of ideotype assumptions is ineffective, there are other sources of germplasm that have been bred for adaptation to the target environment using the other ideotype models. This is very important for a domestication breeding program where the genetic base for a decades-long effort can be selected in a matter of years and in a limited number of environments—a stark contrast to the process of traditional crop domestication, which was a distributed effort taking place over thousands of years and countless diverse environments.

The first few years of perennial flax evaluations will focus mainly on selection of the most vigorous plants, as well as detailed phenotyping, which will allow us to characterize genetic variation of traits relevant to the ideotype. From this, we will begin to quantify ideotype goals for each category. As recommended by Belford and Sedgley (1991), the degree of change must be reasonable to avoid pushing the population too strongly in any one direction [62]. Plants will be grouped by ideotype category and the top performers selected to be used as parents to generate new populations for each breeding objective. Although categorized separately, these populations will be evaluated together, and selection out of the population will proceed regardless of category.

Multiple methods will be used to select elite genotypes. First, especially vigorous, striking, or otherwise unique plants will be selected visually from the population. These selections could be categorized under a particular ideotype, or just selected for general vigor. Next, genotypes which significantly improve towards one or more aspects of the ideotype will be chosen for use in crosses to combine favorable traits. An example of this would be crossing the individual with the least amount of shattering to the line with highest yield per se. Crossing studies will also be performed on top candidate species to determine the feasibility of creating interspecific hybrids to combine favorable traits unique to a given species.

Finally, some individuals will be selected for average performance across all traits of the ideotype. This can be accomplished in multiple ways. First, the traits can be numerically ranked for importance, and then sorted in reverse order, which will place a strong emphasis on the top traits in the list. Another method is to use some form of index selection in which each genotype is ranked based on an overall score. This score can be calculated in multiple ways but it is generally based on the level of performance for each trait, as well as how each trait is weighted relative to the others. One advantage of using index selection over the 'prioritize and sort' method discussed above is that multiple traits can be equally weighted. Especially in the early stages, genotypes may be selected using any of these methods for use as parents.

The populations established from the resulting crosses will allow us to begin assessing features such as combining ability and trait linkage. It will also allow us to begin testing the assumptions of the ideotype model as it applies to perennial flax domestication. For example, does an oilseed population selected for traits such as low shattering, increased branching, and large seed size result in increased yields over time? And how do those yields compare to the plants selected on yield per se? Does selection for yield per se result in unintended morphological/physiological changes to the plant that challenge the ideotype assumptions? These are the type of questions that can be addressed by carefully tracking the methods of phenotyping and selection, as well as overall pedigree. Thus, applying the ideotype approach to domestication of a wild perennial grain crop will allow for careful testing of assumptions about agronomic performance and crop physiology.

8. Contingency

If the initial range of variation observed for key traits is unsatisfactory from a breeding standpoint, the search for germplasm could be expanded to a wider range of sources. Currently, most accessions being evaluated are from the USDA North Central Plant Introduction Center in Ames, Iowa or the Plant Gene Resources of Canada in Saskatoon. Additional genebanks which maintain large collections of *Linum* germplasm (Table 4) could be sources for valuable ideotype traits.

Table 4. List of flax accessions held at germplasm repositories worldwide, sorted by total number of accessions (table adapted from Diederichsen and Richards, (2003)) [38].

Name of Institution	Country	Number of Accessions
All Russian Flax Research Institute (VNIIL), Torzhok	Russia	6100
N.I. Vavilov Institute of Plant Industry (VIR), St. Petersburg	Russia	5700
Research Institute for Technical Cultures (RITC)	China	4000
Breeding company DSV, Lippstadt	Germany	3500
Ethiopian Genebank, Addis-Ababa	Ethiopia	3100
North Central Plant Introduction Center, Ames, Iowa	USA	2800
Plant Gene Resources of Canada (PGRC), Saskatoon	Canada	2800
Research Institute for Cereals and Industrial Crops (RICIC), Funduela	Romania	2700
Other collections (81)		22,300
Total		53,000

9. Conclusions

This paper provides an overview of the applications of ideotype breeding to perennial crop domestication. Domestication requires an involved and very complex breeding effort to capture all target traits in a single organism. A comprehensive model-based approach, such as ideotype breeding, can be therefore be incredibly valuable as an organizational tool. Ideotype models help prioritize multiple traits appropriately for breeding goals and ensure that all traits are considered when making selection decisions. The process of refining the ideotype as new information arises also provides an opportunity for the breeder to regularly apply current technologies or knowledge about the crop towards the breeding goals. While an undomesticated species like perennial flax lacks published knowledge and a long history of prior improvement, it also has the advantages of high genetic variability and the potential for multiple end-uses. Development of a comprehensive flax domestication program will require integrating a wide array of knowledge and expertise from disciplines such as breeding, agronomy, genetics, entomology, food and materials science, horticulture, and environmental science, to name a few. Ultimately, an ideotype model can provide a central organizing principle along which all parties can relate their ideas and knowledge about the progress and direction of the program.

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