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https://doi.org/10.1007/s10722-017-0597-y

RESEARCH ARTICLE

# Dwarf germplasm: the key to giant *Cannabis* hempseed and cannabinoid crops

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Received: 10 October 2017 / Accepted: 29 November 2017

**Abstract** After a century of banishment, both euphoric ("marijuana") and non-euphoric ("industrial hemp") classes of *Cannabis sativa* are attracting billions of dollars of investment as new legitimate crops. Most domesticated *C. sativa* is very tall, a phenotype that is desirable only for hemp fibre obtained from the stems. However, because the principal demands today are for chemicals from the inflorescence and oilseeds from the infructescence, an architecture maximizing reproductive tissues while minimizing stems is appropriate. Such a design was the basis of the greatest short-term increases in crop productivity in the history of agriculture: the creation of short-stature ("semi-dwarf"), high-harvest-index grain cultivars, especially by ideotype breeding, as demonstrated during the "Green Revolution." This paradigm has considerable promise for *C. sativa*. The most critical dwarfing character for breeding such productivity into *C. sativa* is contraction of internodes. This reduces stem tissues (essentially a waste product except for fibre hemp) and results in compact inflorescences (which, on an area basis, maximize cannabinoid chemicals) and infructescences (which maximize oilseed production), as well as contributing to ease of harvesting and efficiency of production on an area basis. Four sources of germplasm useful for breeding semi-dwarf biotypes deserve special attention: (1) Naturally short northern Eurasian wild plants (often photoperiodically day-neutral, unlike like most biotypes) adapted to the stress of very short seasons by maximizing relative development of reproductive tissues. (2) Short, high-harvest-index, oilseed plants selected in northern regions of Eurasia. (3) "Indica type" marijuana, an ancient semi-dwarf cultigen tracing to the Afghanistan-Pakistan area. (4) Semi-dwarf strains of marijuana bred illegally in recent decades to avoid detection when grown clandestinely indoors for the black market. Although the high THC content in marijuana strains limits their usage as germplasm for low-THC cultivars, modern breeding techniques can control this variable. The current elimination of all marijuana germplasm from breeding of hemp cultivars is short-sighted because marijuana biotypes possess a particularly wide range of genes. There is an urgent need to develop public gene bank collections of *Cannabis*.

**Keywords** *Cannabis sativa* · Hemp · Hempseed · Marijuana · Dwarf · Semi-dwarf

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## Introduction

> "One small step for man, one giant leap for mankind."
> —Attributed to astronaut Neil Armstrong when he first set foot on the moon in 1969.

A primer on variation in *Cannabis sativa*

*Cannabis* originated in Eurasia (possibly in central Asia), where domestication in north-temperate areas produced two low-THC gene pools and their hybrids (collectively termed "hemp" and assignable to *C. sativa* L. subsp. *sativa* var. *sativa*) and, in parallel in south-temperate areas, two high-THC gene pools and their hybrids (collectively termed "marijuana" and assignable to *C. sativa* subsp. *indica* (Lam.) Small et Cronq. var. *indica* (Lam.) Wehmer) (Fig. 1). The informal group names given in Fig. 1 corresponds as follows with Small's (2015) nomenclature, which is in accord with the International Code of Nomenclature for Cultivated Plants (Brickell et al. 2016):

European Hemp = *Cannabis* Group European Fiber and Oilseed

Chinese Hemp = *Cannabis* Group East Asian Fiber and Oilseed

Hemp Hybrids = *Cannabis* Group European × East Asian Fiber and Oilseed

Indica Type Marijuana = *Cannabis* Group Narcotic, THC/CBD Balanced

Sativa Type Marijuana = *Cannabis* Group Narcotic, THC Predominant

Marijuana Hybrids = *Cannabis* Group Narcotic Hybrids

In Europe and northern Asia, until about the 19th century, *C. sativa* was grown virtually exclusively for fibre, just occasionally for its edible seeds (also used in

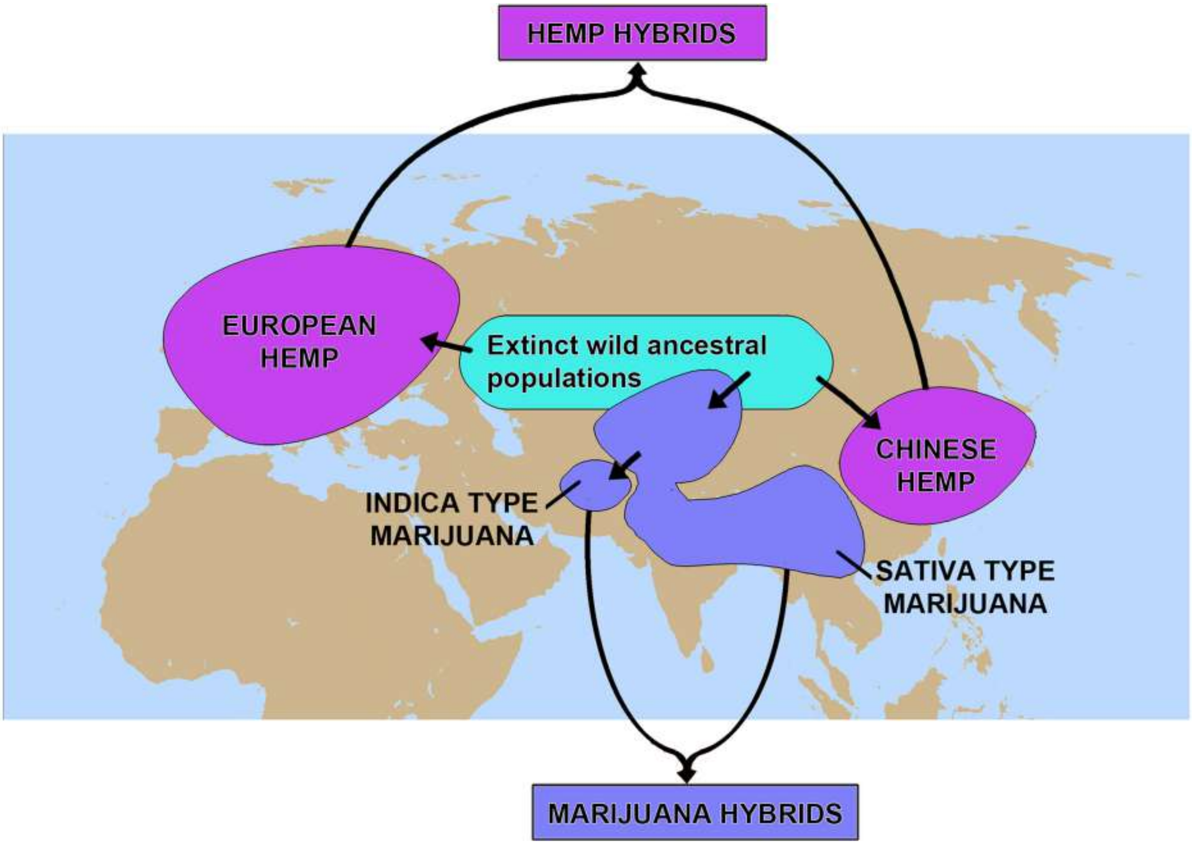


**Fig. 1** Approximate postulated geographical locations of ancestral *Cannabis sativa* and the four principal groups domesticated more than a millennium ago. Hybridization, mostly during the last century, has obscured differences between the low-THC European and Chinese hemp groups, and between the high-THC "indica type" and "sativa type" marijuana groups

the past for lubricating and illumination oil). In southern Asia and Africa, the non-intoxicant uses of the stem fibre and oilseed were also sometimes exploited, but the plants were particularly employed for drugs for recreational, cultural and spiritual purposes. All populations of *C. sativa* appear to be completely interfertile and there are no genetic barriers to interbreeding (Small 1972). Indeed, wide outcrossing produces hybrid vigour. Pollen is distributed by wind over considerable distances, so domesticated kinds need to be maintained by selection or they lose their distinctiveness. Detailed information concerning the evolution, classification, and nomenclature of the four basic domesticated groups is presented in Small (2015, 2016, 2017), and where required for the topics discussed in this paper, necessary background will be provided. Ruderal forms are frequent, most if not all of which likely represent escapes that have re-evolved adaptations for survival outside of cultivation (Small 1975); information on these "wild" populations pertinent to the discussion will also be given.

## Retarded progress

No plant has been more controversial than *C. sativa*. Concern over its harm potential as a source of illegal ("narcotic") drugs led to worldwide governmental suppression of almost all research on it for most of the twentieth century, even for inarguably beneficial products, and many consider that its pariah status in some jurisdictions should be maintained. Indeed, in most Western countries there remain bureaucratic, regulatory and criminal hurdles that are obstacles to scientific investigation and commercial development. Nevertheless, in the last three decades *C. sativa* has been under agronomic development for non-intoxicating applications, notably in Europe and Canada, and the United States appears poised to follow suite (Cherney and Small 2016). Moreover, the authorized production of intoxicant plants for medical and recreational purposes has recently become a multi-billion dollar enterprise in several countries. Unfortunately, development of both intoxicating and non-intoxicating kinds of cannabis suitable for today's marketplace has been strongly retarded by a nearly universal dependence on very tall plants, which as discussed in this review, are inherently inefficient for production of both oilseeds and drugs. An additional issue retarding progress, as will be examined, is that exclusion of marijuana germplasm for the breeding of oilseed cannabis has been very short-sighted because of the invaluable genetic variability of the former. Hopefully this paper will serve not only to familiarize the scientific community with the biological aspects of the cannabis plant necessary for its economic development, but also legislators who are currently addressing how to alter laws and regulations in order to maximize benefits while minimizing harm.

## Ideotype breeding

Plant architecture is commonly defined as the three-dimensional organization of the aerial part of the plant (e.g. Zhao et al. 2015). Crops are grown as large groups of individuals, and so considerations of their architecture usually assume that the plants in question are uniform and evenly spaced (Nair et al. 2013). Donald (1968), who coined the phrase "ideotype breeding," emphasized that breeding of crops, especially cereals, would benefit by first targeting for a presumptively ideal architecture or archetype maximizing the harvested portion, rather than simply directly selecting for yield and against defects. (Donald recognized that other phenotypic features could be included in the ideotype, and subsequent authors more emphatically included physiological contributors to the harvest.) Consistent with Donald's concept, dry matter production and partitioning of yield in relation to crop architecture proved to be critical considerations for the great advances in crop yield that occurred during the "Green Revolution" of the 1960s and 1970s (Tandon and Jain 2004), which were based particularly on introducing dwarfing genes into the two leading crops, wheat and rice. Where the phrase "ideotype breeding" is used in this paper, the intent is to reflect Donald's original emphasis on architecture, not phenotype in general. As stated by Huyghe (1998) "It should not be concluded, however, that only selection on the architectural traits will be sufficient to get high yielding genotypes." For critiques of ideotype breeding, see Rasmusson (1987), Sedgley (1991) and Dickmann et al. (1994). Duc et al. (2015) pointed out that an ideal ideotype in today's world should take account of "other issues such as environmental-friendly, resource use efficiency including symbiotic performance, resilient production in the context of climate change, adaptation to sustainable cropping systems (reducing leaching, greenhouse gas emissions and pesticide residues), adaptation to diverse uses (seeds for feed, food, non-food, forage or green manure) and finally new ecological services such as pollinator protection."

## Semi-dwarf architecture: a key to progress

As discussed in this review, since the middle of the 20th century, the most significant advances in productivity of many of the world's most important grain crop species have been associated with the creation of short-season, large-leaved, short-stature, high-harvest-index cultivars. This paper examines architectural features of *Cannabis* that are similarly likely to contribute to increased productivity. As will be noted, there is an extremely close parallelism within *C. sativa* of such features that contribute to increased productivity in both non-intoxicant ("hemp") plants and intoxicant ("marijuana") plants. Moreover, as will be detailed, before the dawn of modern breeding, highly productive cannabis land races of both non-intoxicant and intoxicant biotypes were selected (likely unconsciously) with the desirable semi-dwarf architectural characteristics.

## Clarification of some terminological issues

The botanical classification of *Cannabis* has been extensively debated, and need not be discussed here (for extensive analyses, see Small 2015, 2016, 2017 for the majority view that the only species meriting recognition is *C. sativa*). However, one technical nomenclatural issue should be understood: the distinction between "cultivars" and "strains." More than a hundred kinds of non-intoxicating *Cannabis* are frequently and justifiably termed cultivars. A very few biotypes of marijuana also meet the technical publication requirements for cultivar status. By contrast, there are thousands of illicit or quasi-licit, allegedly different marijuana "strains" that are currently circulated in the black, gray, and medicinal marijuana trades. However, Article 2.2 of the nomenclatural code for cultivated plants (Brickell et al. 2016) forbids the use of the term "strain" as equivalent to "cultivar" for the purpose of formal recognition. Biologically, many marijuana strains are in fact equivalent to cultivars, although the majority of marijuana strain names are fabrications with no merit.

Another nomenclatural issue that may confuse some readers is the use of "cannabis." Non-italicised, "cannabis" is a generic abstraction, widely used as a noun and adjective, and commonly (often loosely) used both for cannabis plants, any or all of the products made from them, and (sometimes) how they are used.

While kinds of *Cannabis* capable of producing a psychological "high" (euphoria) are often referred to as "drug types," the term is inexact since (as noted below) there are drug (pharmacological) kinds that are not capable of producing a "high" (but nevertheless are effective medically). "Euphoric" and "non-euphoric" are also inexact, since the main intoxicant cannabinoid (THC) is sometimes non-euphoric, and the main non-intoxicant cannabinoid (CBD) can be euphoric (sedative and anodyne). "Intoxicant" or "intoxicating" are the terms adopted in this paper to refer to plants capable of producing a "high." This usage may confuse some readers, especially with a medical background, who have become habituated to employing the term intoxicant as etymologically meaning "toxic," but standard dictionaries make it clear that the word also means "inebriant," and this is the sense that is intended.

## THC regulation—an excessive handicap for non-intoxicating uses

*Cannabis* contains an unusual class of terpenophenolic secondary metabolites, defined as "cannabinoids." Over 150 have been recorded for *C. sativa*, although some are post-biosynthetic transformation or degeneration products (ElSohly and Gul 2014). Delta-9-tetrahydrocannabinol ($\Delta^9$-THC, or simply THC) is the principal cannabinoid of intoxicating forms of *C. sativa*, while cannabidiol (CBD) is the principal cannabinoid of almost all non-intoxicant biotypes. Plants that have been selected for fibre and oilseed characteristics almost always produce limited amounts of THC, but high amounts of CBD. In contrast, plants that have been selected for intoxication are high in THC, and for practical purposes this (and cannabinol, a degeneration product of THC) are the only cannabinoids of significant euphoriant potential.

In the living plant the cannabinoids exist predominantly in the form of carboxylic acids (i.e. a –COOH radicle is attached to the molecule). These decarboxylate into their neutral counterparts (the molecules lose the acidic –COOH moiety, leaving an H atom) under the influence of light, time (such as prolonged storage), alkaline conditions, or when heated. Carboxylated THC (known as THC acid) is only marginally intoxicating. With mild heat (as applied when smoking, vaporising or cooking marijuana), THC–COOH decarboxylates to form $CO_2$ and THC, which is quite euphoric. For simplicity, the discussion in this paper will refer simply to THC and CBD, regardless of whether carboxylated or not.

Intoxicating biotypes of *C. sativa* originated in southern Asia, where they have been grown for spiritual, recreational and medicinal drugs for several millennia. They are the source of marijuana, the world's most widely consumed (usually illicitly) psychoactive drug, although receiving increasing legal acceptance for both medical and recreational usages (Small 2004, 2007). As will be discussed, "sativa type" marijuana strains have considerable THC but no or very little CBD, while "indica type" marijuana strains frequently have substantial amounts of both THC and CBD. Although only high-THC strains are employed for marijuana, concern over the growing use of the plant for inebriant drugs led to most of the Western World banning the cultivation of all forms of *C. sativa* in the early 20th century.

With the conspicuous exception of the United States, by the beginning of the twenty-first century, cultivation of non-intoxicating C. *sativa* for the production of fibre and oilseed products resumed after at least a half century of total prohibition in most Western nations. In most of these countries specific cultivars are authorized to be grown under license, based on a threshold concentration of THC in the reproductive parts of the plant. Although a level of 1% THC is considered a minimum value to elicit an intoxicating effect, current regulations in Canada, most American states, and many other jurisdictions use 0.3% THC dry weight of the infructescence as the arbitrary threshold point, a criterion first established by Small and Cronquist (1976). The phrase "industrial hemp" is now commonly employed to designate fibre and oilseed cultivars of *C. sativa* with very limited THC. The 113th US Congress enacted the Agricultural Act of 2014 ("farm bill," P.L. 113-79), which provided a statutory definition of "industrial hemp" as any part of *C. sativa* with a THC concentration of not more than 0.3%. The European Union lowered this concentration to 0.2%.

For most of the last seven millennia, *C. sativa* has been cultivated in the temperate world almost exclusively as a stem (bast or phloem) fibre crop, and indeed was considered invaluable for fabric and cordage. Today, such usage is obsolescent, and while there are numerous emerging fibre applications (Small and Marcus 2002; Small 2014), the hemp fibre market is minor. Although the oilseed use of *Cannabis* is also quite ancient, it has been extremely limited until recent decades, which have witnessed hempseed exhibiting substantial potential to become a world-class oilseed (Cherney and Small 2016), useful for human food, livestock feed, nutritional supplements, industrial oils, and occasionally as a biofuel (Small 2016).

Cannabinoids for the most part were not chemically characterized until the last half-century. Several are promising for medical applications, and are under intense study (Grotenhermen and Müller-Vahl 2017). In very recent times, as will be noted, biotypes rich in in the non-intoxicating CBD have acquired great interest as this chemical is reputed to have extraordinary health benefits, as well as multi-billion dollar potential.

Regardless of non-intoxicant usage (fibre, oilseed, medicinal cannabinoids), there is or has been interest in breeding biotypes with superior characteristics, and of course germplasm is fundamental for the purpose. However, breeders have effectively been forbidden from accessing high-THC strains for the purpose, and in any event have not considered high-THC strains as usable because of the problem of creating new cultivars with THC that exceeds permitted levels. Nevertheless, this paper presents the viewpoint that in fact marijuana plants represent an invaluable genetic resource for improving industrial hemp. This review especially explores the breeding value of germplasm from short-stature marijuana strains for creation or improvement of semi-dwarf oilseed cultivars, which have far more economic potential than fibre cultivars (Small 2016a; Cherney and Small 2016), and are also suitable as sources of non-intoxicant medicinal cannabinoids.

## Advances in grain crop architecture: models for creating highly productive *Cannabis* cultivars

"Grains" are small hard seeds or one-seeded fruits with dry pericarps, primarily from cereal grasses, occasionally from pulses such as common bean and soybean, and other field crops such as Canola and sunflower. Most grain crops are herbaceous, usually grown as annuals, and (increasingly) machine harvested just once, requiring simultaneous availability of many mature grains. Because grain crops are grown for their sexually-produced small but numerous propagules, they may be recognized as a kind of architectural "form-function category" by comparison with crops cultivated for such other structures as very large fruits, underground parts, aerial stems or foliage. Oilseed hemp is in fact a grain crop. It happens that cannabinoids are also obtained primarily from the reproductive parts of the plant, especially from bracts associated with the flowers and fruits, so that much of the architecture of *Cannabis* that is beneficial for grain production is simultaneously beneficial for cannabinoid production.

All domesticated plants have been modified from their wild ancestors, and field crops have particularly been selected to grow in dense monocultures. To a considerable extent, such selection has been unconscious (Zohary 2004).Today it is feasible to consciously design cultivar architecture for productivity, and because grains represent the majority of human food, grain crops have been especially examined in this regard. Modern crops are cultivated at densities empirically determined to maximize yield efficiency in relation to agricultural inputs. As pointed out by Sangoi and Salvador (1998) "Population density, whether operating directly on the plant or indirectly on biotic factors associated with plant density, is one of the most important factors in determining grain yield… For each production situation, there is a population that maximizes the utilization of the resources available, especially light, water and nutrients, allowing the production of maximum grain yield. Optimum… population for maximum economic grain yield varies with cultivar, row width, soil fertility, soil water and climatic effects." However, these considerations leave unanswered the question of what specific architectural features might contribute to maximizing yield of a given crop species under a wide variety of agronomic conditions.

"Plant architecture" refers to the three-dimensional structure of plants and their organs. Wang and Li (2008) stressed the importance of degree of branching, internodal elongation and shoot determinacy in defining plant architecture. Natural selection has adjusted the development of plants to survive in their wild habitats, but to increase productivity in cultivation humans have altered the previously wild plants by artificial selection. Plant architecture can often be deliberately and usefully changed by modifying soil and climate, employing growth regulators, or pruning. However, the present discussion is concerned with genetically determined, agronomically advantageous plant architectural features. In the case of grain crops, the focus is on assessing spatial layouts and energy allocations of roots, stems and foliage in relation to their contribution to the production of the grain, as well as the spatial positioning of the grain in relation to harvesting.

Although root architecture is doubtless critical to crop performance, most analyses of crop architecture have been concerned with above-ground (shoot) structure. Principal characters that have been measured include determinacy (particularly whether new seeds continue to be produced indefinitely), stem height, internode length, branching patterns (for leaves, flowers and fruits), foliage characteristics (size, shape, angle, canopy coverage), and propagule (seed or seed-like fruit) density (concentrated or scattered), size, and proportion of non-edible material (usually the "hull").

Plant breeders are intimately familiar with the need to address interacting characteristics, albeit the goal may be to optimize a particular trait. In altering plant architecture it is, accordingly, necessary to be aware that concomitant or pleiotropic effects may be induced with respect to stress resistance and market considerations. For example, canopy shading characteristics in soybean can result in different temperatures near the soil which can greatly affect the grain yield (Jaradat 2007). Moreover, a given plant architecture, like other aspects of the phenotype, may be beneficial in one environment, detrimental in another. Nevertheless, the simple goal of altering plant architecture to increase yield has merit.

De Bossoreille de Ribou et al. (2013) wrote "The increase in yield potential through conventional breeding over the past 50 years in maize, rice and wheat resulted from the combined enhancement in harvest index and in light interception efficiency. Increased harvest index has been achieved through dwarfing (shorter, more compact stem) and through improvement in seed set and in fruit and/or seed size." These considerations are examined in the following as guides to the breeding of more productive hempseed cultivars.

## The agricultural benefits of short-stature crops

The terms "dwarf" and "semi-dwarf" are sometimes perceived as offensive, pejorative and politically incorrect, but have become established in the agricultural and horticultural literature, and so now seem unavoidable. ("Semi-dwarf" is conventionally hyphenated, although the hyphen is superfluous since the expression is now an accepted word.) In reference to crops, the distinction between dwarf and semi-dwarf is arbitrary, and depends on the plant under discussion. The Merriam-Webster (2012) collegiate dictionary, in reference to plants, characterizes "dwarf" as "much below normal size" and "semi-dwarf" as "of or being a plant of a variety that is undersized but larger than a dwarf." For fruit trees and ornamental plants, some biotypes may indeed be so small compared to the standard plants that they are appropriately termed "dwarfs" but for most herbaceous crops genuinely tiny plants are probably just too small to be useful, and in most cases the term "semi-dwarf" is applicable. With respect to wheat and rice, the crops for which semi-dwarfism is best known, Dairymple (1980) wrote, "Semi-dwarfism is at once both easy and difficult to define. At one level, it is simply a plant which has a distinctly shorter stalk than traditional varieties… Visually, however, it is sometimes difficult to draw the line… Moreover, each variety varies in height from location to location and from year to year." FINOLA, the world's most popular semi-dwarf hempseed cultivar, is typically about 1.5 m in height at maturity in Canada, whereas almost all other cultivars are 2 m or taller. Of course, "big" and "little" when applied to organisms are not necessarily adequately reflected by height alone, since short things may be massive laterally (note Fig. 24), and tall creatures may be very slim.

"It can be argued that the introduction into cereals of genes to reduce stem height has saved more lives than any other scientific development" (Hedden 2003a). However, the public is largely unaware that the creation of highly productive short-stature crops transformed agriculture, saved billions of people from starvation, and currently most of the world's food calories now come from dwarfed versions of less efficient crops that were grown half a century ago. Indeed, the dwarfing and associated increased productivity of crops that have occurred in recent decades arguably represent the greatest achievement in the ca. 13,000 year history of agriculture. "The benefits associated with semi-dwarfism became a part of mainstream agriculture during the 'Green Revolution,' which greatly improved yields of wheat and rice" (Klocko et al. 2013). (It bears pointing out, however, that Green Revolution crops often require high levels of fertilizers, irrigation and pesticides, and by supporting a much larger human population the world's environmental health is threatened. See Pingali 2012 for a critique.) "In species of agronomic importance, reduction of plant height has resulted in large increases in yield" (Milach and Federizzi 2001). "Semi-dwarfism is a beneficial trait in many crop species… There has been a general world-wide trend to produce semi-dwarf crops of cereals and other crops" (Forster and Shub 2011). The comparative stature of a normal and an early semi-dwarf wheat line are shown in Fig. 2. Comparisons of a generalized crop and a related semi-dwarf derivative are shown in Figs. 3 and 4, and discussed in the following.

Three principal reasons have been advanced why dwarfing plants is agriculturally advantageous. (1) Shorter, sturdier plants are less prone to lodging from wind and rain, and from gravity (short thick stalks can better support a heavy crop of seeds). (2) Dwarfed plants have superior yields because some of the reserves normally dedicated to vegetative growth are redirected towards the harvestable product, particularly grain or fruits, thereby improving harvest index. (3) The grain (fruit or seed) of compact plants is relatively easy to collect because the desired parts are held closely together (Fig. 3), reducing harvesting loss (Figs. 3, 4). Dwarfed plants may also be more efficient in utilization of nutrients and water, but while there may indeed be relative physiological superiority, the simple fact that modern dwarfed cultivars have less non-harvested tissue to needlessly use nutrients and water may account for some of the efficiency.

## Physiology of induction of dwarfism

Some diseased ornamentals are maintained in an infected condition because of the desired dwarfing effect, and bonsai are minitiarized by stunting their

**Fig. 2** Conventional wheat (left) and semi-dwarf wheat (right). These strains, believed to be from the original experiments of Norman Borlaug that led to the creation of semi-dwarf wheat, are maintained by the University of Minnesota. Borlaug's work, for which he received the Nobel Peace Prize in 1970, doubled wheat production in Pakistan, India and Southeast Asia between 1965 and 1970, preventing massive food shortages, and greatly improving world food security Photo by William P. Cunningham University of Minnesota and Mary Ann Cunningham Vassar College. Copyright © The McGraw-Hill Companies, Inc. Reproduced with permission

growth with extreme environmental stresses. These induced pathologies, albeit aesthetically attractive, are hardly desirable techniques for crop production. Orchard trees can often be dwarfed (in order to facilitate fruit harvest) simply by grafting onto a dwarfing rootstock. However most dwarfed crops have been bred for smaller size. "Dwarfism in plants is brought about by an irregularity in one or more of the various growth-related mechanisms, and may involve physical defects in some cellular growth processes, or problems in the production and action of phytohormones" (Ordonio et al. 2014). Gibberellins (GAs) are well known hormones controlling plant growth and development. In several crops, genes producing dwarfism have been identified, and these often act by lowering GAs (Sakamoto et al. 2004), although other mechanisms are known (Turnbull 2005). Several mutations responsible for short stature in wheat and rice have been identified (Hedden 2003b; Sakamoto and Matsuoka 2004), and these relate to GAs. There does not appear to be literature regarding the physiological or genetic control of small stature in *Cannabis*, although the effects of photoperiod on curtailing height development are well-studied, as noted later.

## Allometry and allocation in relation to dwarfism

Some dwarf or semi-dwarf plants aren't simply uniformly smaller with respect to all organs than standard sized relatives, but exhibit several phenotypic changes. In humans, "proportionate dwarfism" refers to all body parts being reduced comparably, while "disproportionate dwarfism" indicates that only selected parts are relatively small. The concept of "allometry" has been extensively applied to animals, for which it can be defined as the study of the relationship of body size to shape, anatomy, physiology and behaviour. Clearly the relative sizes of the parts of an organism, i.e. its allometric relationships, are important to the survival of wild species (Niklas 1994) and to the value of domesticated species. "Allocation" is closely related to the concept of allometry (Weiner 2004) but stresses proportionate sharing of energy (assimilate partitioning) to different parts. For wild animals and plants, the relative

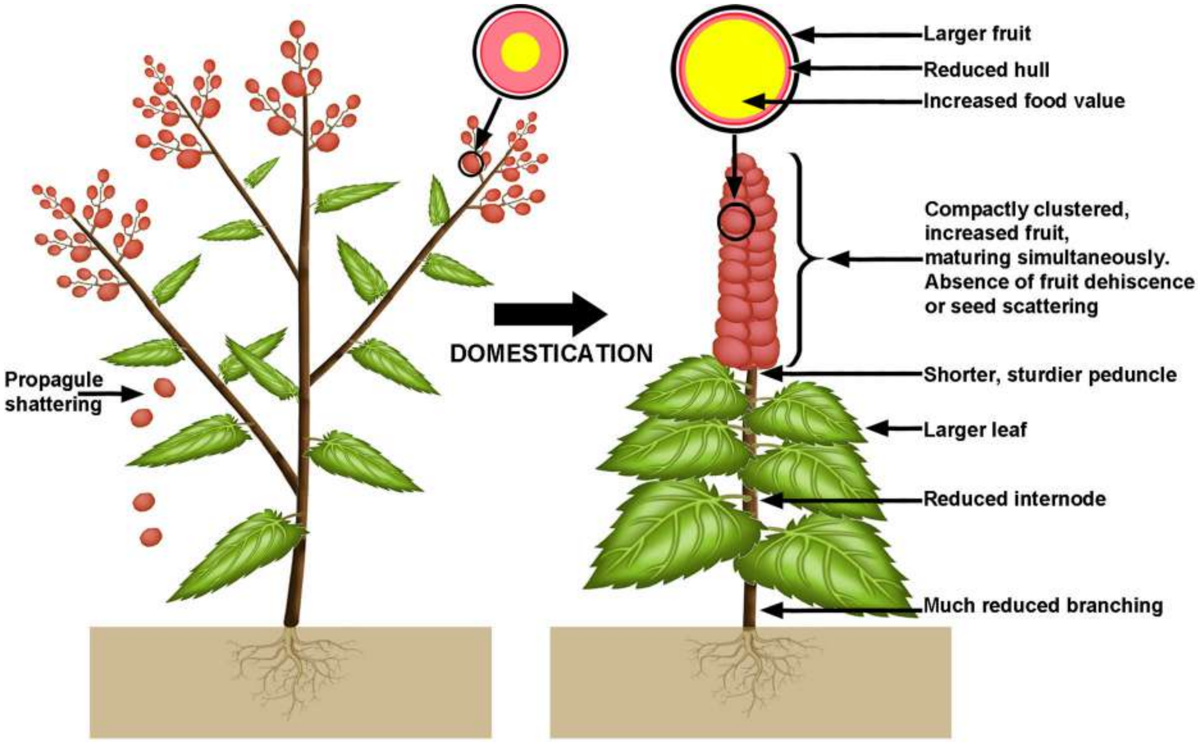


**Fig. 3** A generalized grain plant (left) and an advanced semi-dwarf derivative (right). Characters contributing to higher efficiency of production are labelled and discussed in the text. Prepared by B. Brookes

allocation of resources to reproduction and to other growth functions is critical for survival (Reekie and Bazzaz 2005). For crop plants, maximizing allocation of energy to the desired portion is the key to productivity and efficiency, and is the most important consideration for why crop dwarfism is desirable. In both animals and plants, the relative size of constituent parts results especially from different growth rates, which are substantially genetically determined. However, most plants are much more plastic than most animals, i.e. their development is more strongly influenced by habitat variables. Such environmental considerations are important to determination of relative allocation of the plant's energy to its different parts, but genetically determined characteristics are key to the performance of domesticates.

## Plant size in relation to photoperiod

Many plants are programmed to initiate reproductive structures in response to photoperiod, which accordingly can significantly alter relative proportions of vegetative and reproductive tissues. *Cannabis* is a quantitative (facultative) short-day plant—flowering is normally induced by a required sequence of days each with a minimum uninterrupted period of darkness ("critical photoperiod"). The critical photoperiod required to induce flowers is 10–12 h of light for most hemp cultivars, often 13–14 h for marijuana strains. However, some populations are day-neutral ("autoflowering" in the marijuana literature), particularly at the northernmost locations of survival or near the equator. In all cases, both wild and domesticated populations adapted to local climates (more or less reflected by latitude) come into flower in the fall in time to mature seeds. Whether a given architecture that is most productive for a cultivar adapted to a limited range of latitude is also most productive for cultivars adapted to other latitudes is unclear, but it does seem intuitive for annual plants like *C. sativa* that some balance of growth of the various parts of the plant may be appropriate for a wide range of latitude, and this is an underlying assumption of much of the following discussion.

**Fig. 4** A generalized grain crop (left) and an advanced semi-dwarf derivative (right) in field format. Spatial advantages of the latter include condensed area of the plants facilitating precise regulation of density, and concentrated location of fruit facilitating machine harvesting. Prepared by B. Brookes

## Reduction in stems to allocate more energy to desired tissues

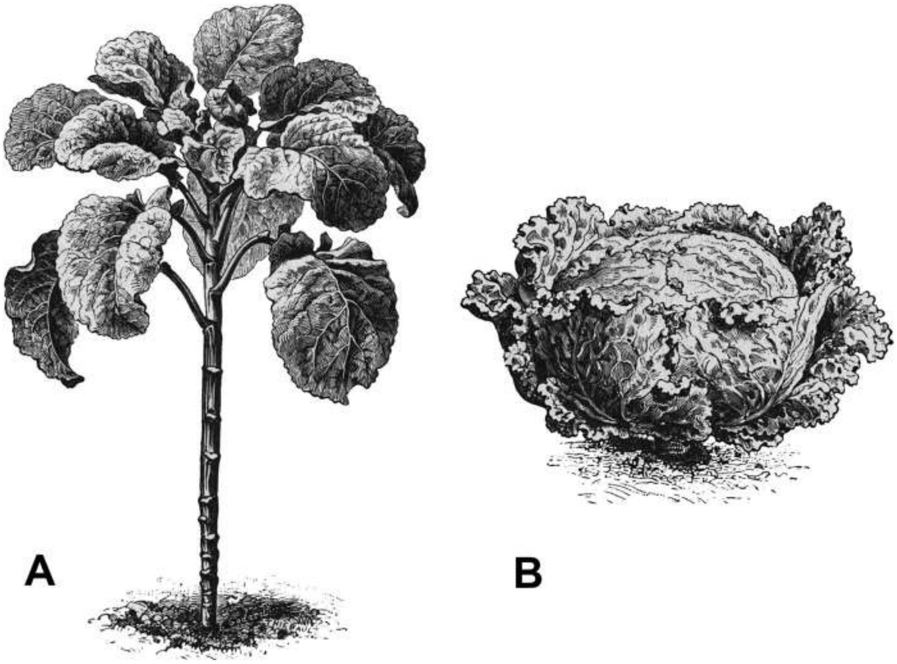
If foliage and stems are the only products of interest, breeders may wish to maximize one at the expense of the other depending on their relative commercial values or purpose. For example, cabbages (*B. oleracea* var. *capitata* L.; Figure 5B) are advanced forms of *Brassica* with highly reduced stems, compared to their more primitive relatives kales (*B. oleracea* var. *viridis* L.; Figure 5A). Because cabbages do not divert their energy into uneaten stems they produce more food for humans, although not for livestock, which readily consume the stalks of kales.

Sorghum (*Sorghum bicolor* (L.) Moench) presents a similar situation. Modern grain sorghum cultivars intended for human food tend to be relatively short—about a metre—because of two or three dwarfing genes, introduced to reduce problems of harvesting taller plants (Carter et al. 1989; Ordonio et al. 2014, Fig. 6B). By contrast, "sweet sorghums" (grown for syrup from the stem), and cultivars grown for forage or ethanol are much taller (Fig. 6A) but have comparatively small seed heads.

## Reduction in stems supporting foliage: a key to maximizing light interception in field crops

Photosynthetic energy capture is a critical limiting factor for agricultural productivity, and in crops this is the function of leaves, assisted by stems which orientate the foliage to sunlight. Stems serve to minimize competition for sunlight among the plant's own leaves and to compete for light with nearby obstacles, particularly other plants. The leaves of an individual plant often rival each other for sunlight, and to reduce such auto-competition, many plants develop branches in order to separate the leaves and maximize overall exposure to sunlight. Shrubs and trees grow tall because this shades out competitors, but at the cost of allocating considerable energy to stem tissues. When plants are grown closely together, such as in forests and crop monocultures, light penetration decreases vertically as successively lower leaves reduce light intensity, with the result that the lower leaves become progressively less efficient, and may even drain rather than contribute to photosynthate accumulation. Farmers have learned by trial and error how densely particular biotypes should be grown to maximize

**Fig. 5** Extreme reduction of stems in *Brassica* illustrated by comparing a primitive "tree cabbage" or "kale" (**A**) and an advanced "head type" cabbage (**B**). *Source*: Vilmorin-Andrieux (1885)



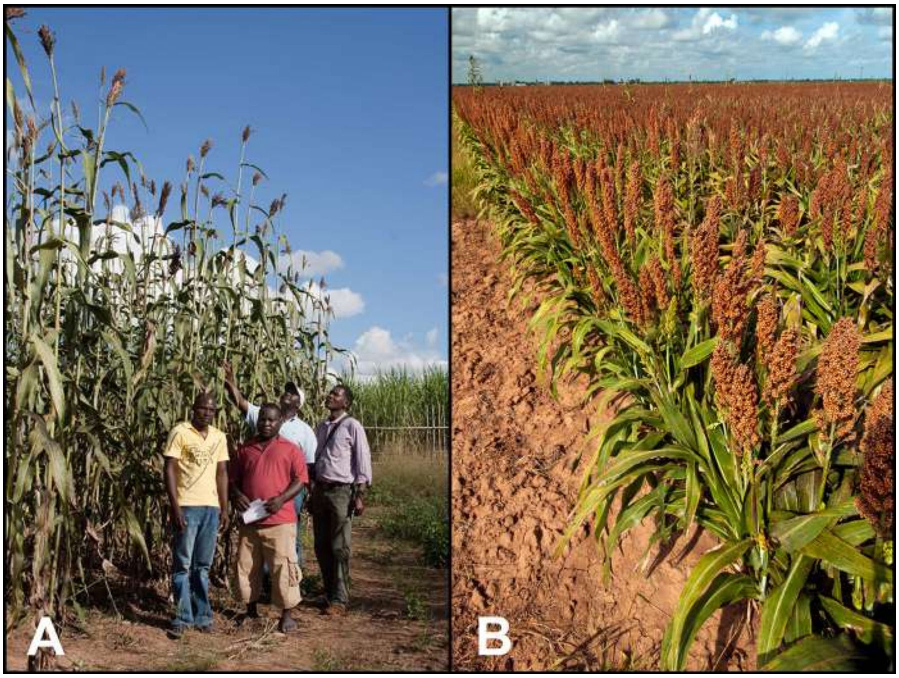


**Fig. 6** Variation of stems in sorghum (*Sorghum bicolor*). **A** Tall form ("sweet sorghum") grown for stem syrup and biomass in Mozambique. Note small inflorescence and long internodes. Photo by Swathi Sridharan, ICRISAT (CC BY 2.0). **B** Semi-dwarf grain form grown in Texas. Note massive infructescence and short internodes. Photo by Bob Nichols, USDA (CC BY 2.0)

production. To optimize a crop's efficiency of energy capture on an area basis, presumably there is an ideal layout of foliage (canopy structure), which in turn is related to relative proportions of photosynthetic tissues (leaves) and non-photosynthetic tissues (stems). It may be desirable to select biotypes which maximize foliage while minimizing supporting stems on an area basis, and this could be a key advantage of dwarfed crops.

Crop architecture governs reception of light for photosynthesis. When plants are grown at high densities, sunlight will only penetrate a canopy for a certain depth. In tall cultivars, this may mean that the lower leaves photosynthesize inefficiently for lack of light. Plants that are short but compact, even when planted very closely together, may represent the best way of capturing sunlight on a field area basis. The key advantageous architectural feature in many semi-dwarf crops may simply be to maximize photosynthetic leaf area while minimizing non-photosynthetic stems that support foliage and reproductive tissues.

Modification of foliage architecture under domestication has been critical to increasing grain yield in major crops. De Bossoreille de Ribou et al. (2013) observed that "The increase in yield potential through conventional breeding over the past 50 years in maize, rice and wheat resulted from the combined enhancement in harvest index and in light interception efficiency… Increased light interception efficiency has required the development of larger-leafed cultivars and better arrangement of leaves… Soybean cultivars from the United States… intercept almost 90% of the photosynthetically active radiation, and allocate 60% of the biomass energy-equivalent to seeds." (Harper et al. 1970 indicated that most grain crops allocate about 30% of their annual net photosynthetic assimilation to reproductive effort.)

Sarlikioti et al. (2011) studied the architecture of greenhouse tomatoes in relation to light absorption and photosynthesis. They found that increasing leaf length:width ratio or increasing internode length increased both light interception and photosynthesis. They also concluded that there may be more than one architecture for maximizing productivity. It is quite uncertain whether such findings can be generalized to other crops, or whether the traits that maximize efficiency need to be established for each individual crop.

In nature, the size of plant leaves has been selected not just to maximize photosynthesis but also to reduce damage from insects and wind, a circumstance in which smaller (but more numerous), narrower leaves seem to be adaptive (Small 2016, Chapter 6). The foliage of crops is frequently larger than the corresponding leaves of their ancestors (Small 2016, Chapter 6), and as will be seen this trend is observable in *C. sativa*. As reviewed by Mathan et al. (2016), genes have been identified in rice that increase leaf blade width and accordingly yield.

However, simply increasing leaf area index (ratio of leaf area to growing area occupied) does not take account of leaf angles, which affect exposure to sunlight. Truong et al. (2015) noted that post-Green-Revolution, higher-yielding cultivars of rice and maize have smaller leaf inclinations compared to pre-green revolution biotypes. When the leaves are packed together closely, transpiration rate is likely to be reduced, and this may influence photosynthesis, especially when water is limited. Heat load could also be altered (reduced because of shading, increased because of lowered evaporative cooling). Studies of interacting foliage characteristics in relation to productivity are needed for *C. sativa*.

An appropriate light-collecting architecture may differ depending on location. In tropical areas, overhead light of very high intensity is often encountered for part of the day, while in temperate areas where *C. sativa* is much more frequently encountered the light is of comparatively low intensity and is directed at an angle. In the case of indoor-grown marijuana, light is considerably lower than outdoors, and growers limit the height of plants (usually by controlling flowering time).

## Reduction in stems supporting flowers and fruits: another key to allocation of energy to desired tissues

In addition to assisting foliage to orientate to sunlight (discussed in the previous section), stems also serve to assist flowers to orientate to receive or distribute pollen by wind or animal vectors, and to assist propagules to be exposed to wind or animal vectors for distribution. The latter two functions are relatively easily controlled in cultivation, and so plant breeders often sacrifice stem tissues making up the reproductive parts of the plant in favour of more desirable tissues. The following example illustrates this.

Several forms of *Brassica* (especially but not exclusively *B. oleracea* L.) have been selected for flower edibility (the flowers do not develop normally, but remain immature, and they as well as floral stalks produce succulent, undifferentiated tissues; for discussion, see Munro and Small 1997). Broccoli raab (*B. rapa* L. em. Metzg. subsp. *oleifera* (DC.) Metzg.; Figure 7A) has small floral clusters on a highly branching axis. By comparison, in broccoli (*B. oleracea* var. *italica* Plenck; Fig. 7B) the branches (at least the internodes) have been reduced considerably, and in cauliflower (*B. oleracea* var. *botrytis* L.; Figure 7C) the only concession to normal stem tissue is the subtending peduncle at the base of the massive condensed head. This set of vegetables illustrates well how human selection has resulted in crops (broccoli and cauliflower) with an increased proportion of the reproductive tissues making up the plant, much less tissue dedicated to normal branches, and compaction of the reproductive tissues into a centralized mass that can easily be harvested, transported, processed and consumed.

When the desired product is reproductive tissues, such as flowers, fruits, and seeds (as in *C. sativa*), the optimum architecture is a balance of foliage and stems (and roots) that divides energy transfer to the reproductive organs in a manner that maximizes production efficiency on an area basis, not necessarily a per plant basis, and also takes into consideration variables such as ease of machine harvesting, timing of ripeness, and time of consumer demand. As argued in this review, except for yield of fibre, semi-dwarfs with minimized internodes represent the most desirable crop architecture for *C. sativa*.

## Correlates of reduction of internodes

"Brachysm" is dwarfness characterized by shortening of the internodes, and is a key consideration in creating semi-dwarf versions of otherwise tall crops. Mutations producing brachytic sorghums are well known (Hadley et al. 1965, Fig. 6B). Semi-dwarf cultivars are often more compact, because the internodes are shorter, so that foliage, flowers, and fruits are packed into a more condensed space. In nature, packing the flowers closely together could make pollination less likely, but in cultivation this factor is easily controlled. In nature, packing the fruits and seeds closely together could make their natural distribution less likely, but in cultivation it makes them easier to harvest.

## What can be learned from the breeding of hop (*Humulus lupulus*)?

Hop (*Humulus*) is the nearest genus to *Cannabis*, and in view of their relatively close genetics it seems worth examining breeding of dwarfism in the former for clues about its prospects in the latter. The common hop (*H. lupulus* L.) is the source of hops ("cones" or "strobili", these are usually inflorescences, sometime infructescences), which are very much like marijuana "buds" (which are also inflorescences, as noted later). Both products are produced from female plants, commonly maintained vegetatively. Elite marijuana strains are propagated by cuttings producing annuals,

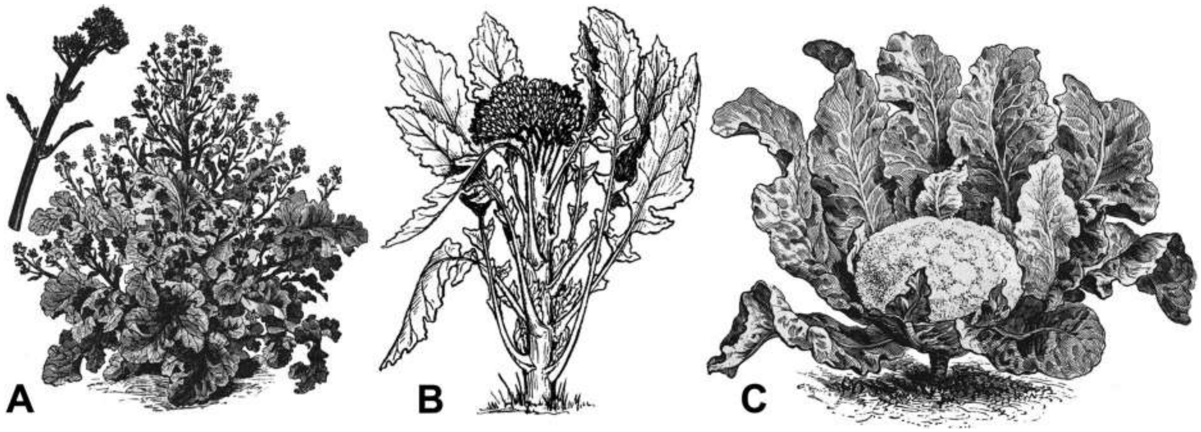


**Fig. 7** Inflorescences of *Brassica oleracea* plants selected for edible inflorescences. **A** Broccoli raab (sometimes called "rapini"), with relatively small floral clusters on a highly branched inflorescence (figure **A** and **C** are from Vilmorin-Andrieux 1885). **B** Broccoli, with several major branches of tightly clustered flowers (figure by Pearson Scott Foresman, released into the public domain). **C** Cauliflower, with one massive tightly clustered inflorescence

and hop cultivars are clones propagated by perennial rhizomes. The common hop is a high-climbing vine that regrows annually. It is normally trained to climb up to horizontal trellises 6 m or more in height. Semi-dwarf selections (conventionally called "dwarf hops;" Fig. 8B), growing to 3 m or less have appeared on the market for cultivation on "low trellises" (2.3–3 m in height; Fig. 8A), and have proven to be much more productive than conventional hop cultivars grown on low trellises (Neve 1991). The initial commercial dwarf varieties, 'First Gold', 'Herald' and 'Pioneer', were registered in 1996, followed by 'Pilot' in 2001 and 'Boadicea' in 2005 (Darby 2005). The semi-dwarf cultivars are advantageous in allowing hand-picking or the use of much shorter machine harvesters, they are easier and less costly to erect, reduce labour costs, and facilitate spraying for pests and diseases, and so they are desirable much like so-called dwarf fruit trees. Patzak et al. (2013) found that complex changes in growth and stress hormones were responsible for the dwarfism of 'First Gold' dwarf hop. The most obvious trait of dwarfed hop cultivars is short internodes. Additional characters contributing to productivity were determinacy (cessation of growth of the terminal stem apex while still quite short) and early start of production of flowers (starting at lower, rather than at higher nodes) (Henning et al. 2017). These three features constitute suggestions for parallel ideotype breeding for short stature in *Cannabis*.

## The strategy of reduction of males in domesticated *Cannabis*

Less than 10% of flowering plants are dioecious (Divashuk et al. 2014), but an appreciable number of perennial crop species are dioecious (e.g. asparagus, date palm, hop, kiwifruit, nutmeg, papaya, persimmon, pistachio, strawberry, yam). Annual dioecious plants are notably rarer than perennial dioecious plants (Anonymous 1859), and there are very few annual dioecious crops like *C. sativa*, (common spinach, *Spinacia oleracea* L., is another example) suggesting that the phenomenon of annual species with separate males and females is strategically inconsistent with efficient agriculture. Common spinach is grown for the vegetative portion, and until recently the same was true for *C. sativa*, and it does seem that when a

**Fig. 8** Conventional and dwarf hop (*Humulus lupulus*). **A** A comparison of an early experimental dwarf hop on a low trellis (left) and a normal hop on a high trellis (right). **B** 'First Gold', the first dwarf hop cultivar and the breeder, Peter Darby. Photos courtesy of Dr. Peter Darby, Wye Hops

dioecious annual crop is grown for the reproductive portion of just one of the sexes, the harvest is compromised. Wild *Cannabis* populations are virtually always dioecious, with about half of the plants possessing male flowers only, and half with female flowers only (the result of an X/Y/autosome sex determining mechanism; Ainsworth 2000). In livestock agriculture, only a few males are maintained for breeding animals for food, since the females are much more docile and often produce a valued product such as milk, eggs and offspring. Staminate (male) *Cannabis* is similarly of limited value, because males are relatively weak plants that die after they shed their pollen whereas females produce inflorescences (for marijuana and cannabinoids) and infructescences (for seeds). The males take up expensively maintained space that could be better utilized by females and they interfere with mechanical harvesting.

Male cannabis is less detrimental as a fibre crop than as an oilseed or cannabinoid crop. Fibre cannabis is usually harvested well before seeds are formed, and both male and female plants of dioecious fibre cultivars provide useful fibre. In past times when labour was cheap, male plants were harvested earlier than the females, and although males produce less fibre, it is of superior quality. However, the different maturation times of males and females (males typically peak in flowering time about 2 weeks earlier than females) and their different architecture are undesirable for ease of harvest and uniformity of product.

As a result of the undesirability of male plants, recently bred commercial cultivars of hemp (both for fibre and oilseed) are usually monoecious, often predominantly producing female flowers (male flowers, when present, typically are at the top of the plant, developing before the female flowers). For the most part, monoecious cultivars of *Cannabis* usually do not have 100% of plants develop uniformly with respect to proportion of male and female flowers, and one often finds some plants that are completely or nearly completely male, and others that are completely or nearly completely female (a phenomenon sometimes termed "subdioecy"). Regardless, monoecious cultivars essentially represent the elimination of male plants.

In the industrial hemp industry, occasionally a hybridization technique is employed to generate $F_1$ seeds which produce plants with only or mainly female flowers. This is accomplished by hybridizing female plants of selected dioecious lines with pollen from monoecious lines (Bócsa 1998; Clarke and Merlin 2016). With some combinations that have been tested for sex-inducing properties, the $F_1$ generation is completely female. The first such unisexual hemp cultivar was registered in 1965 as UNIKO-B. The production of exclusively unisexual hemp as first generation hybrid seed is expensive, and only marginally competitive at present. Open pollination of selected combinations produces "female-predominant" seeds that generate plants some of which have male flowers, but mostly female flowers. Unlike dioecious cultivars, but like monoecious cultivars, generation of seeds employed to sell to growers is a continuous struggle by breeder-suppliers, who must constantly rogue out plants that are male or mainly male.

Marijuana has traditionally been obtained from populations from which all males have been removed, since pollen results in seed production, considered very undesirable. Today, most marijuana is generated by vegetative reproduction of elite female clones. Recently, hybridization techniques are being employed to produce so-called "feminized seed" (a marijuana trade term), offered in the black and gray markets to produce female or mostly female plants. Such seeds could be produced in the same manner as described above for unisexual hemp cultivars. Usually, however, a different technique has been employed because of the much smaller scale (most marijuana growers have not planted large fields) and the existence of elite female clones. Hormones are applied to elite female clones to produce some male flowers, which are employed to fertilize the female flowers. This is a more elaborate method than described above for generating female-producing hemp seeds, but the marijuana trade sells feminized seed for high prices. Feminized marijuana seed will normally be useful for marijuana production, but rarely produces plants which are as good performers as the best elite strains propagated vegetatively. However, "synthetic seeds" of elite marijuana strains, generated by tissue culture (Lata et al. 2009, 2010, 2011, 2012), now has the potential of providing growers with a plant that is extremely uniform for desired female characteristics.

For breeding cultivars, male plants are of course necessary. (Stresses or chemicals can be employed to force females to produce male flowers, but *Cannabis* is quite susceptible to inbreeding depression.) Since the economic products of *Cannabis* are produced by females or at least female-predominant plants, their attributes are the breeder's ultimate concern.

Dioecious *Cannabis* has some advantageous over monoecious forms. Monoecious cultivars are inherently unstable, sex expression varying considerably, and sporadically producing male plants which tend to return the population to the original dioecious state, necessitating continuing rogueing of the males (Faux et al. 2014). While the trend in breeding oilseed biotypes has been towards monoecy (i.e., elimination of males), some breeders continue to produce dioecious cultivars because of their naturally superior vigour. However, this is at a cost: in a cultivated field setting, *Cannabis* produces huge amounts of pollen—far more than is needed—so dioecious cultivars necessarily waste energy by producing far more males than required. The male plants are like drones in a honey bee colony—providing reproductive services but representing a drain on resources—and like drones they die soon afterwards leaving the females to carry on. Male cannabis plants are characteristically slimmer and less vigorous than females (although taller), often with smaller leaves, and in senescence their foliage wilts, shrinks and/or falls, allowing better light access to the females at a time when their photosynthetic demand is great for maturing seeds. Nevertheless the persisting dead males represent an appreciable loss of productivity. While monoecious cultivars solve this problem, a possible alternative is breeding of biotypes in which the males are very slim, occupying little space. Breeding of short males is not a desirable objective, since the males need to present their pollen as high as possible to be transported by the wind, and this would be very difficult if the males were notably shorter than the females.

## Grain size versus grain number as breeding objectives for oilseed hemp

Yield is the most important breeding objective in grain crops, and it may be influenced by various plant architectural features. Particularly relevant are grain size and quantity, which are often negatively correlated (Alonso-Blanco et al. 1999). Mao et al. (2010) noted that "Grain yield in many cereal crops is largely determined by grain size." Kesavan et al. (2013) and Zhang et al. (2014) also observed that grain yield in cereals can be increased by increasing grain size.

In domesticated forms of *Cannabis*, thousand-seed-weight generally varies from 17 to 25 g, but ranges between 8 and 67 have been recorded (Watson and Clarke 1997; Small 2016). Most advanced hemp cultivars have been selected for fibre yield, and these do not differ much in oilseed potential (Mölleken and Theimer 1997). By contrast, some drug strains (which have been selected for prodigious production of flowers), when left to go to seed can yield a kilogram of seeds on a single plant (Clarke and Merlin 2013). Piluzza et al. (2013) reported that the seeds of fibre cultivars are larger than those of drug strains, which is consistent with fibre plants having a more extensive historical food usage for seeds than those of drug forms. Seeds of monoecious cultivars are usually smaller than those of dioecious cultivars, presumably because of inbreeding depression. Clarke and Merlin (2013) pointed out that some Chinese oilseed biotypes grown for eating out of hand produce especially large fruits. However, cultivars of crops selected for large fruit size to be sold in markets may have lower yields than cultivars of the same crops selected for total grain yield. Indeed, it appears that a larger yield of achenes rather than larger achenes is the principal criterion that has been employed to date to select oilseed land races. Deliberate breeding for oilseed yield is very recent, and it remains to be seen which of increased grain size or grain number will optimize yield.

## Secretory gland size and number as breeding objectives for cannabinoid crops

The most fundamental way that plants domesticated for high-THC production differ from wild *C. sativa* and from plants domesticated for either fibre in the stem or oilseed production is simply in gene (allelic) frequencies favouring THC rather than CBD biosynthesis, a subject discussed later. However, while these genes determine the qualitative cannabinoid profile, the quantity of cannabinoids produced is related to size and density characteristics of the secretory glandular trichomes of the plant (Fig. 9).

The cannabinoids of *Cannabis* are synthesized almost only in the heads of secretory epidermal trichomes. The trichomes differ in length of basal stalk and in size of the glandular secretory heads. Most

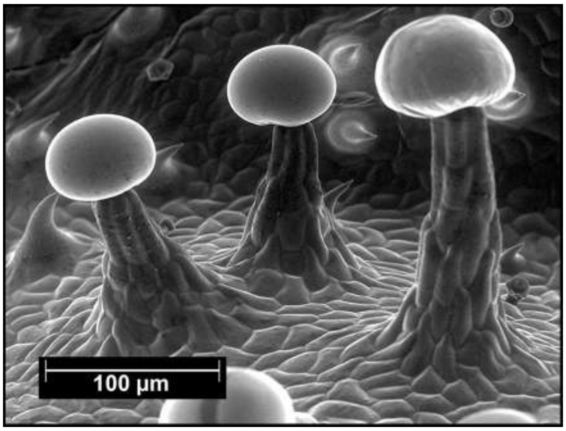


**Fig. 9** Glandular secretory trichome glands on a perigonal bract (the single bract covering each female flower) of a high-THC form of *Cannabis sativa*. Prepared by E. Small and T. Antle

of the cannabinoids are formed in the largest trichomes (Fig. 9), which are found in the female inflorescence, particularly on the "perigonal bract," which is at the base of the female flower, and eventually expands (if the flowers are fertilized) to form a much larger cover for the achene. High concentrations of secretory glands also occur on the very small leaves (usually unifoliolate) that occur near the flowers. Most of the contents of the glandular heads are terpenes, but these and the accompanying cannabinoids constitute a sticky material appropriately termed "resin." The volume of resin (and cannabinoids) produced depends on the number and size of the secretory glands. Clarke (1998) observed that marijuana varieties differ widely in the size of the glandular trichomes. However, there seems to have been selection for concentration and distribution of the secretory glands, with very large densities of the glands and larger glands present on the perigonal bracts of some strains. Various authors (e.g. Soroka (1978; Turner 1981a, b; Petri et al. 1988) have reported that density of glandular hairs on leaves and/or bracts of *C. sativa* is positively correlated with quantitative content of cannabinoids. Small and Naraine (2016) found that a sample of currently marketed elite medical strains possessed much larger trichome secretory gland heads in the inflorescence (possessing gland heads with over four times the volume) compared to wild biotypes and industrial hemp cultivars. Virtually no deliberate breeding focus has been given to date on these secretory glands for purposes of improving cannabinoid crops. Secretory glandular trichomes occur on the surface of about 30% of all vascular plants, and it has been suggested that breeding for them in economic species such as those producing essential oils would be beneficial (Glas et al. 2012). Andre et al. (2016) suggested breeding for cannabinoids biosynthetic pathways to improve productivity. However, simply selecting for gland size and density could be easier. Contrary to this view, Szabó et al. (2010) found that glandular hair density was only weakly correlated with content of carvacrol, the key flavour ingredient of oregano (*Origanum vulgare* L. subsp. *hirtum* (Link) Ietsw.). Although the gland heads of *C. sativa* are only the size of pin heads, they clearly are the dominant part of the plant that needs to be considered when the desired product is one or more of the cannabinoids. Secretory trichome density and gland head size are appropriate criteria for ideotype breeding, albeit they are not directly related to semi-dwarf stature, the primary concern of this paper. All of these criteria require access to germplasm resources, which as will be discussed are very limited.

## Compact versus diffuse inflorescences and infructescences in domesticated *Cannabis*

Aside from stem fibre and biomass, all other significant harvested products of *Cannabis* are generated by the reproductive portions associated with the female flowers and fruits. The perigonal bracts subtending the female flowers are the principal source of economic chemicals (cannabinoids; also terpenes for aromatic products to a very minor extent), and the achenes are a valued oilseed. Therefore, breeders concerned with improving either chemical or oilseed production of *Cannabis* need to focus on inflorescences and their flowers and/or infructescences and their fruits.

Undomesticated *C. sativa* develops female reproductive structures mostly on the ends of branches, so that the resulting seeds are well-separated. Moreover, the flowers and seeds mature sequentially. These developmental features represent survival strategies to prevent (1) a large standing crop of ripened seeds on the plants, and (2) concentrations of seeds at particular locations on the plants, both of which would be extremely attractive to herbivores, particularly birds. Humans, by contrast, prefer crops to develop large standing concentrations of mature forms of the desired product (usually seeds or fruits), since these factors facilitate harvest. In this regard, there are two contrasting architectural strategies that need to be examined: centralization of the reproductive parts in a large compact axis, or development of the reproductive parts in several smaller compact structures on different branches. The branches that subtend flowers and fruit utilize energy reserves of the plant, and hence it is important to consider their design for cannabis plants intended for harvest of flowering parts (i.e. for marijuana) and for harvest of seeds (i.e. for oilseed).

Maize (corn) is particularly instructive insofar as concentration of reproductive parts is concerned. Major cereals such as rice and wheat are low-growing plants, and basal branching (tillering) is one of the architectural features promoting productivity in some cultivars (Yang and Hwa 2008). Like *C. sativa*, however, modern maize (*Zea mays* L. subsp. *mays*) is a tall single-stalked plant. In its evolution from teosinte (*Z. mays* ssp. *parviglumis* H.H. Iltis and Doebley; see Piperno et al. 2009; Ranere et al. 2009), the vegetative part of modern maize has become highly unbranched, while the fruiting parts have become very highly concentrated (Fig. 10). A gene suppressing branching in corn has been identified (Doebley et al. 1997).

Whether harvest is mechanized or by hand is a critical crop architectural consideration. In past times, arable land was often not as scarce as is the case today, and cheap manual labour for harvest was normally available. Accordingly, old land races generally are quite inferior to modern cultivars in respect to efficiency of productivity on an area basis, as well as with respect to suitability for machine harvesting. Aside from fibre hemp, there are very few biotypes of *Cannabis* that have been selected for these modern requirements as field crops.

For the production of hempseed (Fig. 11D), as will be noted later, the recent marketplace strongly favours the development of short plants producing single, very compact infructescences (Fig. 11C). To achieve this architecture, both apical (upward) and axillary (outward) growth are limited. The short, compact plants provide uniformity of field layout and greatly facilitate harvest (compare Fig. 11A, B). Curiously, Small et al. (2007) observed that damaging the stem leader results in considerable branching at the point that the apical meristem is destroyed, and that this actually increases seed production on per plant basis, but at the cost of production on an area basis, which is the ultimate efficiency criterion.

The herbal marijuana market at present is dominated by the production and sale of "buds," i.e. portions of inflorescences made up of very compact, crowded flowers and supporting very short subtending branches along with bracts (Fig. 12C, D; the plural of

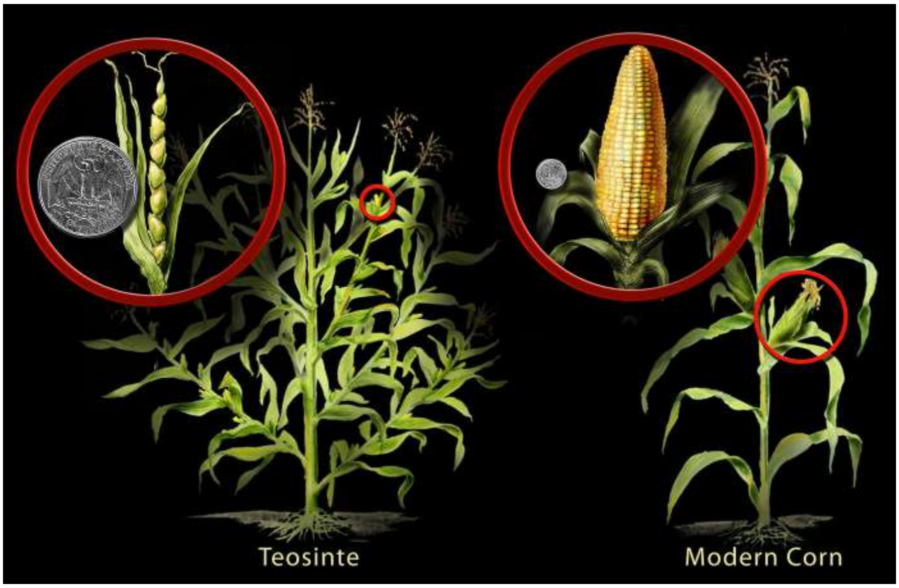


**Fig. 10** Comparison of modern corn and its ancestor, teosinte *Credit*: Nicolle Rager Fuller, National Science Foundation

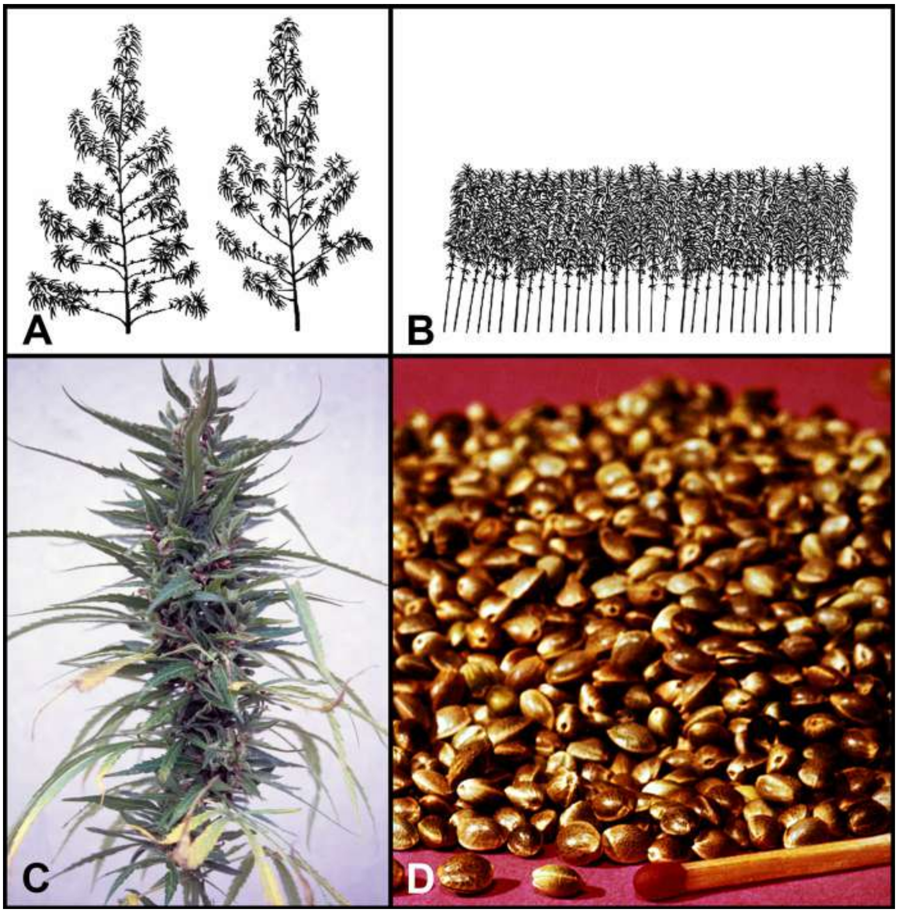


**Fig. 11** Architecture of oilseed hemp. **A** Field profile of a tall biotype grown at low density for seed production. This illustrates traditional production of seeds employing well-spaced plants, which become quite branched and produce many flowers and seeds. However, harvest of the seeds from widespread locations on the plant is difficult, and the plant has diverted much of its energy into production of stems. **B** Field profile of a short biotype with a dense, compact infructescence, grown at high density for seed production. By comparison with A, the concentration of seeds facilitates their harvest, and the reduced stem production diverts more of the plant's energy into seed development. **C** A compact, elongated infructescence, ideal for seed harvest. **D** Mature seeds (achenes). (Drawings by B. Brookes, photos by E. Small)

bud is either bud or buds). These typically contain between 10 and 20% THC, and often the largest of the small (usually unifoliolate) leaves near the flowers are trimmed away ("manicured") to increase the THC content (a selling criterion). Some producers crumble the material, but most purchasers currently mistrust the quality of fragmented material. Illicit marijuana producers harvest and prepare bud entirely by hand. Large-scale authorized producers sometimes use machines to assist these processes, but harvest and processing of bud is still mostly by hand labour, and is responsible for a substantial proportion of the cost of marijuana. A variety of growth and pruning techniques can be employed to modify the size of buds and how they are subtended, and certainly breeding of appropriate biotypes would be more efficient. However, breeding for increased efficiency of mechanical processing (indeed, even to make hand harvesting more efficient) is at a rudimentary stage, and the industry closely guards relevant research and technological information. Indoor cultivation, which is required as a security measure for marijuana production in many jurisdictions, is far more expensive than field cultivation, so biotypes requiring less labour would be welcome. There is good reason to expect that, just as the best strategy for field hempseed utilizes short plants with single, large compact reproductive axes, the same would be best for indoor bud production (compare Fig. 12A, B; also note Fig. 25H). Outdoor marijuana production has largely been an illicit activity to date, but authorized field cultivation is being undertaken in some countries. Probably the same considerations regarding the ideal inflorescence structure for bud harvest apply as for indoor cultivation.

In addition to herbal marijuana, there is a large, growing market for solvent extracts (including so-called "oils") of the cannabinoids, especially for incorporation into edible and pharmaceutical products. The harvest strategy in this circumstance may be

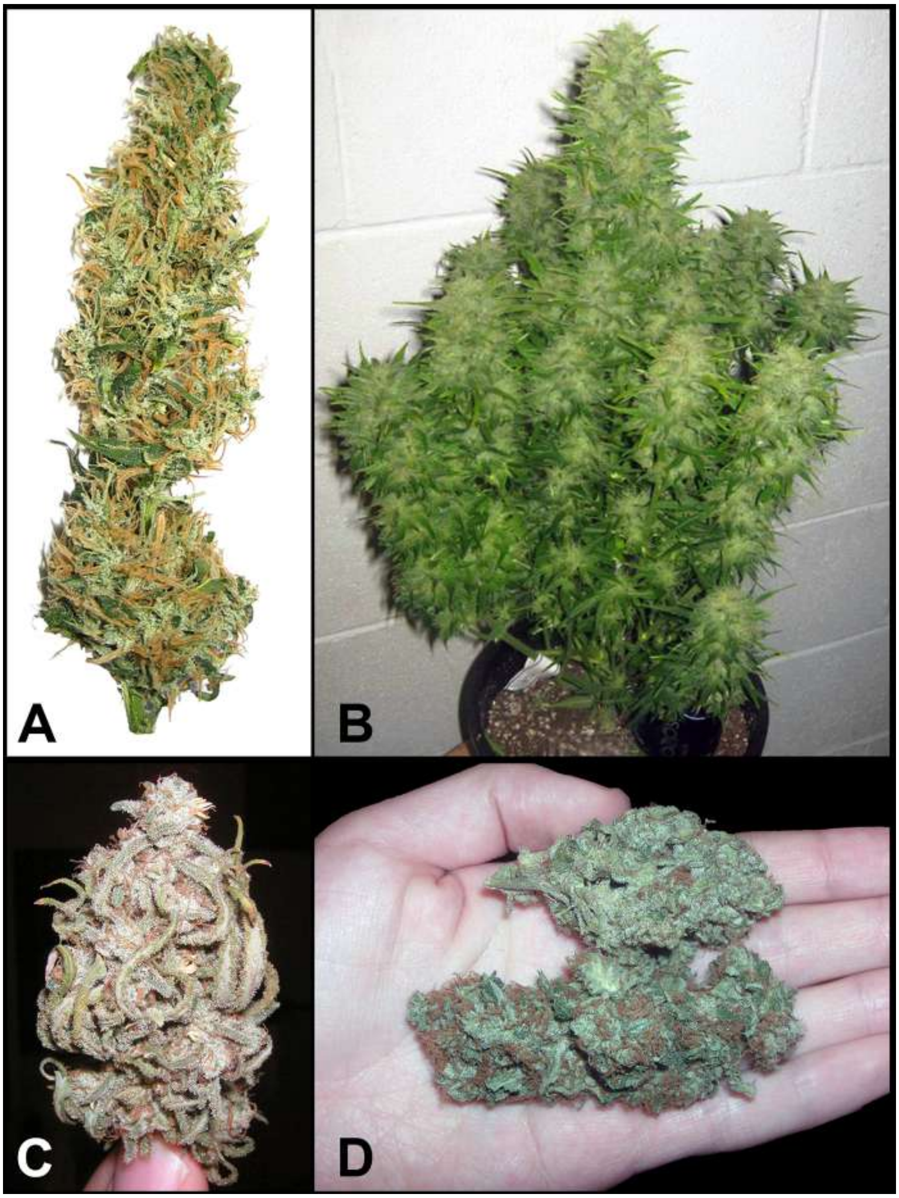


**Fig. 12** Architecture of marijuana strains used to produce "buds" (portions of unfertilized, congested female inflorescences). **A** Inflorescence developed as a single congested axis. (Photo by Erik Fenderson, released into the public domain.) **B** Highly branched plant bearing numerous but relatively small buds (Photo by Chrisgedwards; CC BY 3.0). **C** Bud of the strain Blue Dream. Photo by Psychonaught (released into the public domain). **D** Buds of the strains Platinum Bubba (on top) and Skywalker OG (on bottom). Photo by Coaster420 (released into the public domain)

compared to a fruit that has two market niches, one for the whole fruit market, the other for processed products such as jams and beverages. Whole fruits need to be large, and cultivars not satisfying this criterion are at a disadvantage, even if they produce a much greater yield. Just what kind of marijuana strain architecture is best for maximizing solvent extracts remains to be determined. Moreover, as noted later, foliage can also be employed to provide extracts.

## Architecture of fibre hemp, and why it is unsuitable for the oilseed and marijuana markets

For most of recorded history, *C. sativa* has been grown mainly for stem fibre, and so architectural features maximizing fibre harvest were selected. A wealth of land races were domesticated for fibre, and until very recently legitimate plant breeders of the species were almost exclusively concerned with producing fibre cultivars. The fibre is most efficiently collected from the main stalk, hence fibre biotypes are tall—usually over 2 m (Fig. 13). Since the stem nodes tend to disrupt the length of the fibre bundles, thereby limiting quality, plants with long internodes have been favoured. Fibre strains have been selected to grow well at extremely high densities, which increase the length of both the internodes (contributing to fibre length) and the main stem (contributing to fibre bundle length) while limiting branching (making harvesting easier).

**Fig. 13** Tall hemp fibre cultivar 'Petera' (photo courtesy of Anndrea Hermann)

Selection for fibre quality has resulted in strains that have much more of the highly desirable primary phloem fibre and much less woody core than encountered in marijuana strains, oilseed cultivars and wild plants. Fibre varieties may have less than half of the stem made up of woody core, while in non-fibre strains more than three quarters of the stem can be woody core (de Meijer 1994; Fig. 14A). Moreover, in fibre plants more than half of the stem exclusive of the woody core can be fibre, while non-fibre plants rarely have as much as 15% fibre in the corresponding tissues. Also important is the fact that in fibre selections, most of the fibre can be the particularly desirable long primary fibres (de Meijer 1995). Another strategy has been to select stems that are especially hollow at the internodes (Fig. 14B), with limited woody core, since this maximises production of long phloem fibre. While the decrease in woody tissues makes the stems less resistant to lodging by wind, fibre plants are always grown at great density, so the plants provide lateral support for each other. However, plants grown for seeds or resin are always grown at much lower densities, and therefore fibre biotypes are not suited to withstand lodging well when grown for other purposes. The limited branching of fibre biotypes is often compensated for by possession of large leaves with wide leaflets (Fig. 15), which increase the photosynthetic ability of the plants.

Of course, farmers require seeds to grow fibre crops, and so fibre plants are necessarily capable of producing a crop of seeds. When fibre biotypes are cultivated for seed, they are grown at low densities in order to promote branching, and therefore flowers and seeds. However, *Cannabis* plants that have been selected for production of fibre often have low genetic propensity for flower production and seed output. Biotypes with architectural features specialized for concentrating the plant's energy into production of fibre inevitably do so at the cost of production of reproductive tissues, whether seeds (for oilseed production) or floral bracts (for cannabinoid production).

Aside from architectural considerations, fibre cultivars lack quality parameters of seed cultivars (such as fatty acid profile) and marijuana strains (fibre cultivars produce much less resin, very little of the desired THC, and frequently have terpenes with a less acceptable odour).

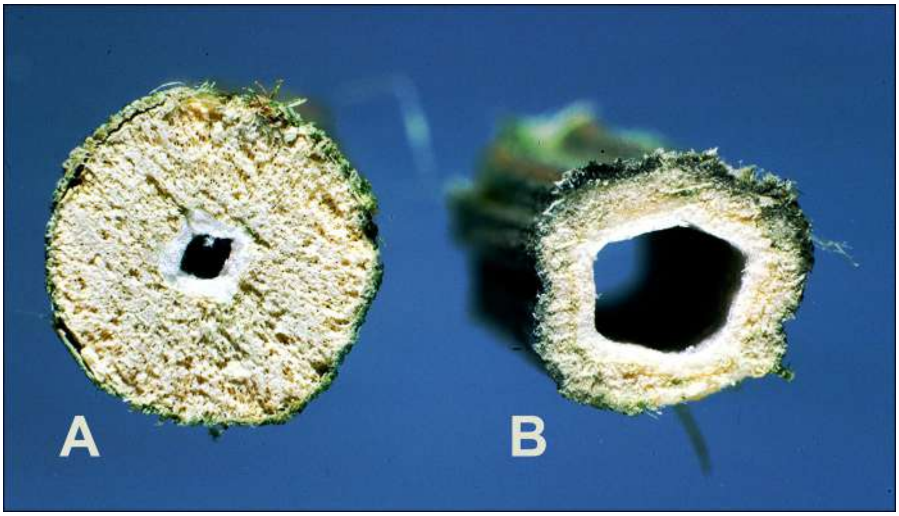


**Fig. 14** Cross sections of stems of *Cannabis sativa* at internodes. **A** Marijuana plant. **B** Fibre plant. Fibre cultivars have stems that are hollower at the internodes, i.e. with less woody tissues, since this allows more energy to be directed into the production of phloem fibre

**Fig. 15** A large leaf with wide leaflets of a fibre cultivar. Plants grown for fibre are cultivated at great density so they have few branches, and limited foliage. Thus they require large leaves to supply energy to the plants (the very large size of some leaves represents physiological compensation for lack of other leaves on the plant, not just the genetic propensity to grow large)

## Architecture of wild hemp and dual purpose (fibre-oilseed) hemp, and why they are unsuitable for the oilseed and marijuana markets

As illustrated in Fig. 16A, wild (ruderal) plants of *C. sativa* under good growth conditions can become very highly branched from a main stalk, and the same applies to numerous landraces that have been grown for general purposes (i.e. both for stem fibre and oilseed; Fig. 16B). “Dual purpose” cultivars compromise the production of both fibre and oilseed. For purposes of producing reproductive tissue products (marijuana, seed) the considerable branching of dual purpose forms represents a huge wastage of energy diverted into stem production.

## Architecture of conventional tall outdoor marijuana, and why it has limited suitability for the marijuana market

Most cannabis plants grown outdoors for marijuana are naturally tall and branched (Fig. 17), a morphology much like open-grown wild and fibre biotypes (Fig. 15). In past times, although leaves are relatively low in THC, the foliage, as well as the inflorescence was employed to a much greater extent for drugs than accepted in today’s market. (The elimination of foliage is one of the main factors responsible for the observation that today’s marijuana is much stronger

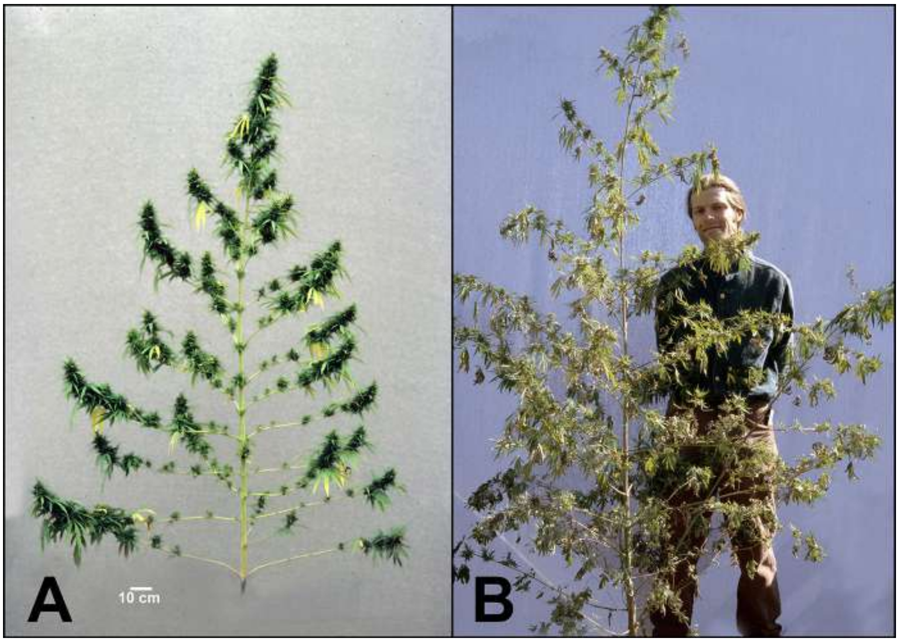


**Fig. 16** Architecture of open-grown female plants of relatively unselected forms of *Cannabis sativa*, illustrating the huge proportion of the plant dedicated to stems, and the very diffuse distribution of the reproductive tissues. **A** A weedy plant cultivated near Toronto, Canada, from seeds from Georgia (Eurasia). **B** A dual-purpose (fibre-seed) landrace, cultivated near Toronto from seeds from China

**Fig. 17** Conventional tall marijuana plants. Photo by E. Small

than in past decades). Except for the smallest (unifoliolate) leaves, most of the foliage contains relatively low amounts of THC, and today it is primarily inflorescence branches ("buds") that are marketed. The very large production of foliage and stem tissue in proportion to the inflorescences in most marijuana plants indicates a very inefficient harvest index for production of marijuana. Most people viewing very large marijuana plants interpret them as impressive models of proficient drug production, when in fact the reverse is true.

## Sources of semi-dwarf *Cannabis* germplasm

This section identifies four extant classes of biotypes that can supply genes associated with dwarfism in *C. sativa*.

1. Northern low-THC ruderal populations

In the northernmost areas of distribution of ruderal *C. sativa*, particularly in Siberia, the limited season only allows small plants to develop. The plants are programmed to come into flower and develop seeds before a killing frost. They tend to be quite short (less than a metre) and unbranched (Fig. 18) although in fertile soils their growth is more substantial. In the marijuana trade, such plants are often referred to as "*Cannabis ruderalis*," and because they are often day-neutral ("autoflowering") they have been employed in marijuana breeding programs to transfer this trait to marijuana strains. Although they are natural dwarfs, they carry considerable "genetic baggage" that makes them well-adapted to their very stressful northern habitat, but poor parental material for breeding better biotypes.

2. Semi-dwarf low-THC oilseed selections

*Cannabis sativa* is employed as a source of a multi-purpose fixed vegetable oil, obtained from the "seeds" (fruits, technically achenes). The true "seed" portion is enclosed within the fruit wall (pericarp), which in combination with the seed coat forms the protective "hull" or "shell." Most of the seed is filled by an

**Fig. 18** Herbarium collections of northern dwarf wild ecotypes of *Cannabis sativa*. **A** Type specimen (a female) of *C. sativa* var. *spontanea* Vavilov. **B** Type specimen of *C. ruderalis* Janischevsky (female at left; a male is at right)

embryo, principally the two cotyledons, which are rich in oils, proteins and carbohydrates, upon which the germinating seedling relies for nourishment. A rudimentary nutritive tissue (endosperm, rich in aleuron bodies, which are protein storage organelles) is also present. Hemp seeds contain virtually no THC (Mölleken and Husmann 1997). Beginning in the 1990s, the seeds have become an important commercial source of edible oil.

However, for most of history the seeds were of very minor economic importance, and by the middle of the twentieth century, commercial use was negligible, and cultivated plant selections suitable for dedicated oilseed production were virtually unavailable until the 1990s. For most of the twentieth century the seeds were usually employed as wild bird and poultry feed, although occasionally also as human food. World hemp seed production (mostly in China) fell from about 70,000 tonnes in the early 1960s to about 34,000 tonnes at the beginning of the twenty-first century.

From time immemorial, China has been the world's major producer of hempseed. Small and Marcus (2000) examined the growth of Chinese hemp land races, which are often large. quite branched, and productive of numerous flowers (Fig. 16B), and so capable of high yield of seeds. It appears clear that considerable branching is a characteristic that farmers traditionally stressed in order to maximize seed production. Such an architecture makes harvest difficult, because the seeds are not centralized, and they mature over an extended interval, but in the past, hand rather than machine collection was standard and cheap labour was available. Moreover, the need to maximize production on an areas basis was lesser, and so plants could be grown at lower densities to promote branching. Additionally, the plants could be harvested not just for seeds but also for fibre. Dewey (1914) noted that a Turkish type of land race called Smyrna was commonly used in the early twentieth century in the US to produce birdseed, because it was quite branched, producing many flowers and hence seeds. Indeed, Dewey's description of Smyrna is reminiscent of the well-branched kind of Chinese land race shown in Fig. 16B. For most of history, it seems that tall, highly branched "dual purpose" plants were the source of hemp seeds. In temperate regions of the world, the dual purpose plants would have been employed both for fibre and oilseed, while in more southern areas, plants were likely employed mainly for drugs, but occasionally also for fibre and oilseed.

Until very recent times, the widespread cultivation of hemp *primarily* as an oilseed was largely unknown, except in pre-World War II Russia. The cultivation of hemp as an oilseed crop reached a zenith in nineteenth and early twentieth century Russia, when, in addition to the edible uses, the seed oil was employed for making soap, paints and varnishes. It is uncertain whether the kind of Russian land races once grown as oilseeds are still extant. It is difficult to reconstruct the type of hemp plant that was grown in Russia as an oilseed crop, because (1) such cultivation has essentially been abandoned; and (2) land race germplasm in the Vavilov Research Institute (St. Petersburg) seed bank, the world's largest governmental cannabis seed collection, has been extensively hybridized (Small and Marcus 2003; Hillig 2004) due to inadequate state support for maintenance. Land races certainly were grown in Russia specifically for seeds, and Dewey (1914) gave the following information about such a biotype: "The short oil-seed hemp with slender stems, about 30 inches high, bearing compact clusters of seeds and maturing in 60–90 days, is of little value for fibre production, but the experimental plants, grown from seed imported from Russia, indicate that it may be valuable as an oil-seed crop to be harvested and threshed in the same manner as oil-seed flax." The semi-dwarf oilseed cultivar 'FINOLA', discussed below, was bred from two accessions in the Vavilov germplasm collection.

At the close of the twentieth century, oilseed hemp began to take on increasing economic importance, particularly in Canada but also in Europe, as the hemp industry realized that it had greater potential than hemp grown for fibre. For some time, dual purpose cultivars were grown, because dedicated oilseed cultivars were simply not available. 'FINOLA' (formerly known as 'FIN-314'), the first modern oilseed cultivar, was bred in the mid-1990s from northern Russian stocks (Callaway and Laakkonen 1996). It quickly became the most widely grown cultivar in the Western World for production of oilseed. The plants are short, with dense fruiting stalks, and they evenly fill up a field (Fig. 19). This is dioecious, and it is one of the parents of a number of recently bred similar monoecious cultivars. The recent focus of hempseed breeders has been to develop cultivars that are similar to FINOLA, with high seed

**Fig. 19** Field of *Cannabis sativa* ‘FINOLA’, the first modern hemp cultivar developed exclusively for grain. The low stature facilitates machine harvest and the limited branching minimizes production of stem tissue while allowing a substantial number of plants to be grown in a given area, maximizing production on an acreage basis. The breeder, J.C. Callaway, is shown (photo by Anita Hemmilä, Finola Ltd., permission to reproduce provided by both)

yields, low stature, early maturation, and a desirable fatty acid spectrum (especially higher levels of stearidonic acid and gamma-linolenic acid). It appears that modern hempseed breeders intuitively or intentionally reconstructed the kind of plant that used to be grown in Russia for oilseed, and may in fact have employed some of the original germplasm.

The new hempseed cultivars reflect well the harvest index advantages of grain production, discussed earlier. Plants with limited (or at least compact) branching are naturally superior to irregularly branching plants for the purpose of fully and uniformly occupying a field, and maximally utilizing solar irradiation. Low stature is desirable in oilseed selections to avoid channelling the plants’ energy into stem tissue, in contrast to fibre cultivars for which a very tall main stalk is desired. The ability to grow in high density as single-headed stalks with very short branches bearing considerable seed not only maximizes harvest index but also facilitates mechanized harvesting. Compact clustering of seeds also promotes retention of seeds. And the more or less simultaneous seed maturation also lessens harvest loss from seed shattering.

### 3. “Indica type” high-THC marijuana landraces

“Sativa type” and “indica type” marijuana strains are two discernibly different groups of high-THC cannabis plants domesticated in Asia. The ancient distribution of these is shown in Fig. 1, where it is suggested that the indica type probably arose from the sativa type. Indica type strains were once localized in Afghanistan, Pakistan and NW India. Sativa type strains dominated ancient southern Asia, and more recently became distributed in much of the world, and now are predominant in the illicit trade of Western nations. Extensive hybrids have been generated between the two kinds, to the detriment of the survival of the much less common indica type (Clarke and Merlin 2016). Strains of the sativa type are characteristically tall and well branched in good growing conditions (Fig. 20B), and tend to have relatively narrow leaflets (Fig. 22A). Indica strains tend to be short (about a metre in height) and compact, especially under the often inhospitable conditions under which they are typically grown in Asia (Figs. 20A, 21). They have large leaves and wide leaflets (Fig. 22B). The appearance is often reminiscent of a miniature, conical Christmas tree.

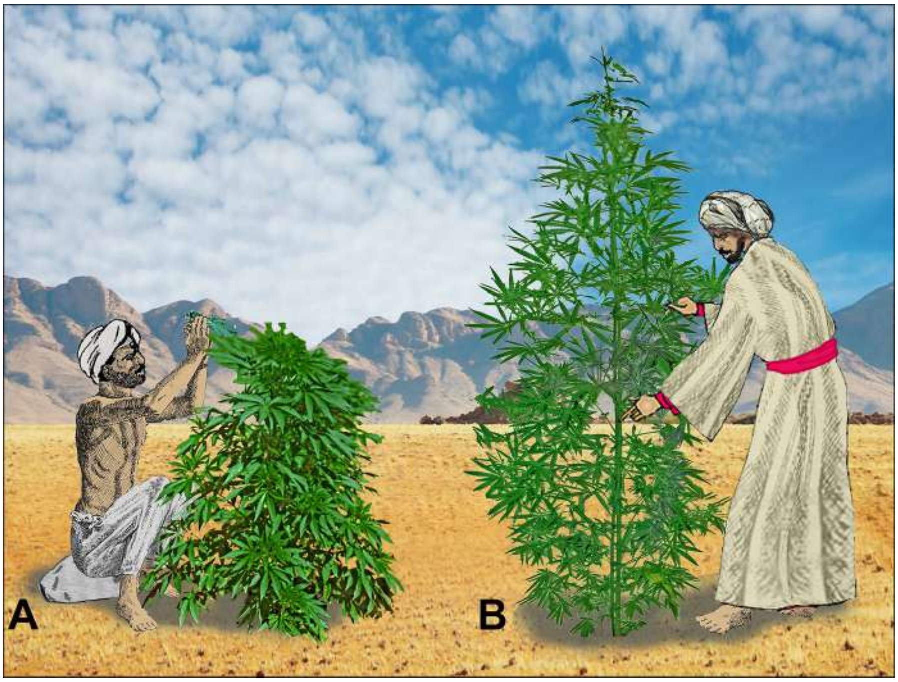


**Fig. 20** Contrast of types of marijuana plant. **A** short compact "indica type." **B** tall diffusely branched "sativa type." Prepared by B. Brookes

**Fig. 21** The short-stature "indica type" of plant in a cultivated marijuana field in Kandahar, Afghanistan in 1971. The late Professor R.E. Schultes is shown with a female plant at left and a male at right. Photo courtesy of N.P. Schultes

**Fig. 22** Contrast of foliage of the two basic kinds of marijuana plant. **A** "Sativa type" leaf with narrow leaflets. **B** "Indica type" leaf with wide leaflets. Photo by Transmitdistort (CC BY 3.0)

More detailed information about the differences between these two classes of marijuana plants is available in Clarke (1998), Clarke and Merlin (2013) and Small (2016). Sativa type marijuana strains originated from relatively low (sometimes semi-tropical) latitudes, compared to cultivars grown for fibre and oilseed, which are adapted to more northern (temperate) areas. As a result, the sativa type strains tend to be photoperiodially adapted to a relatively longer season. They may also be adapted to warmer conditions than most hemp biotypes. However, the indica type strains tend to be earlier-flowering, comparable to oilseed cultivars. Clarke (1998) and McPartland and Guy (2004) interpreted indica type strains as having evolved in the cold, arid regions of Afghanistan and western Turkmenistan, and explained their short height as an adaptation to the relatively short growing season. Because indica type marijuana strains seems to have originated from arid areas, they are not adapted to high-humidity climates, and when exposed to very most conditions their dense flowering tops retains moisture and succumb to diseases of moist areas such as "bud mould" caused by *Botrytis cinerea* and *Trichothecium roseum* (McPartland et al. 2000).

Sativa type marijuana strains characteristically have no or small amounts of CBD, but very high THC levels, and represent the most intoxicating biotypes of the species *C. sativa*. By contrast, strains of the indica type group frequently have moderate levels of both THC and CBD in their cannabinoid profile, i.e. they are less inebriating than sativa type strains. Usage of the term "sativa" to indicate extremely intoxicating plants while using the term "indica" to indicate less intoxicating plants is quite inconsistent with the reverse taxonomic usage of the same terms, and this has led to considerable confusion (McPartland and Guy 2017). The higher THC in sativa strains explains their greater popularity, although they are harder to grow indoors where room height is limited, because of their tallness. Hybrids between the two groups have proven to be well adapted to indoor cultivation and are progressively being marketed (Clarke and Watson 2006).

The characteristics of indica type marijuana are highly consistent with those of an advanced cultigen. Like modern oilseed cultivars, they are short and compact, an architecture reducing diversion of energy into stem production and increasing harvest index for the desired product (inflorescence). Even the foliage (with very large, wide leaflets) is consistent with the trend described earlier of advanced cultigens often manifesting larger leaves than their wild and more primitive cultivated relatives. When indica type strains are allowed to set seed (they are normally harvested for flowering material) the infructescences are very dense, preventing most of the seeds from falling away and being distributed naturally—another indication of considerable domestication.

## 4. Clandestinely-bred high-THC indoor marijuana strains

Law enforcement pressure for the last half-century has had the unintended effect of driving marijuana production indoors where it is harder to detect. Tall plants are frequently too large for covert cultivation in houses, especially when overhead lighting and ventilation are installed in a room. The result has been that smaller, faster-maturing plants with greater proportionate production of flowering material have been selected by illicit breeders and cultivators, especially in the Netherlands and North America, since the early 1970s (Fig. 23). In some cases, indica type marijuana strains were employed as initial breeding material, but it does seem that strains now available arose from a wide variety of marijuana land races. Since this work was done illegally, documentation of the breeding history of most marijuana strains is unavailable or unreliable. "Breeders continue to develop early-maturing and high-yielding varieties that are short and compact for indoor grow room use and to avoid detection outdoors" (Clarke and Merlin 2013). Legitimate, authorized medicinal marijuana growers also often find tall plants to be too awkward to raise in greenhouses and specially fitted secure rooms, and accordingly are also interested in the selection of plants that are naturally short, and so growable under artificial light in small rooms or to accommodate low ceilings.

The height of most indoor marijuana plants can easily be controlled by photoperiod, a dark diurnal cycle of 12 h usually sufficing to initiate flowering, which essentially terminates growth in height. Most outdoor plants are at the mercy of the photoperiod at a particular latitude, and indeed growers can control height of *C. sativa* by deliberately cultivating plants with known propensities to come into flower at given daylight regimes. However, merely hastening maturation by photoperiodic induction is inappropriate for generating an ideal harvest index, and exposing the plants to a long-night regime significantly reduces photosynthesis.

Indoor marijuana growers sometimes resort to removing the tops, pinching stem buds to promote branching, trellising, and other techniques to limit the height of plants (Clarke 1981). Potter (2009) observed that the height of indoor plants can be shortened by growing them under continuous light, or by brushing the plant in early development (like plants buffeted by wind, the stems become thicker and shorter to resist movement). These techniques are effective, but are labour-intensive and a less satisfactory solution than biotypes that naturally produce desired architectures.

**Fig. 23** Short-stature marijuana plants being grown surrepticiously in a confined height-limited space. Illicit breeders have selected such compact strains to avoid detection. US Government photo

Chemical control of height and/or maturation is sometimes practiced for some crops, but is inappropriate for marijuana, for which organic production is now considered essential.

## Vavilov's Law of Homologous Series in relation to the parallel selection of hempseed and marijuana domesticates

Both indica type marijuana strains and the recently bred oilseed hemp cultivars have remarkably parallel architectures: they are short, compact plants, with congested reproductive parts, and large leaves with wide leaflets—all characteristics that are reflective of advanced domestication compared to their ancestral forms, which share contrasting architectures: tall, well-branched plants, with diffusely distributed reproductive parts and smaller leaves with narrow leaflets. This parallelism appears to be consistent with Vavilov's Law of Homologous Series (occurrence of parallel variability of homologous characters in related taxonomic groups; Kupzow 1975). The basis for the parallelism seems clear: oilseed and marijuana have been independently selected for different reproductive parts (respectively for infructescence and inflorescence), but the features maximizing production of both are largely the same.

## Aspects related to the transfer of genes from marijuana to hemp

The hemp industry has been at pains to emphasize that "hemp is not marijuana," i.e. that they are different, a slogan intended to avoid the stigma attached to marijuana. However, this obscures the fact that the indica type of marijuana has genes that may be invaluable for the improvement of oilseed hemp, since both have been selected for similar characteristics. Indeed, marijuana strains represent a much greater range of diversity than do hemp landraces and cultivars, so the potential for marijuana germplasm to improve hemp biotypes is appreciable (by contrast, the potential for hemp germplasm to improve marijuana biotypes is limited).

### THC regulations as a barrier to progress

A critical problem for hemp improvement is that current cultivars (mostly European), the basis of most hemp breeding today, are inbred and have a long history of selection for fibre production. By contrast, there is enormous variation among marijuana biotypes, which should be considered for hemp breeding. However, in most jurisdictions where hemp is cultivated, current regulations virtually prevent the use of marijuana strains to breed improved hemp, because the former are very high in intoxicating THC, and cultivars are permitted to develop only low amounts. Indica type marijuana strains frequently have lower THC levels than the sativa type of marijuana, although nevertheless much higher than currently accepted for licensed cultivation. Regulatory barriers that make it difficult for hemp breeders to utilize high-THC marijuana strains are a major obstacle to exploitation of the vast germplasm resources in intoxicant kinds, although the growing acceptance of medical and recreational marijuana is likely to increase accessibility of marijuana strains for hemp breeding.

### Inheritance of cannabinoids

Sytnik and Stelmah (1999) suggested that CBD and THC are controlled by closely linked but independent genes. Inheritance of the key cannabinoids THC-acid and CBD-acid (respective precursors of THC and CBD) was found to be apparently determined by the allelic status at a single locus (referred to as B) (de Meijer et al. 2003; Mandolino et al. 2003; Pacifico et al. 2006). De Meijer et al. (2003; cf. Mandolino and Ranalli 2002; Mandolino et al. 2003; Mandolino 2004) found evidence that THCA development in *C. sativa* is under the partial genetic control of codominant alleles. Allele BD is postulated to encode CBDA synthase while allele BT encodes THCA synthase. This genetic model holds that plants in which CBDA is predominant have a BD/BD genotype at the B locus, plants in which THC is predominant have a BT/BT genotype, and plants with substantial amounts of both THCA and CBDA are heterozygous (BD/BT genotype). De Meijer and Hammond (2005) found that plants accumulating CBG have a mutation of BD (which they term $B_0$) in the homozygous state that encodes for a poorly functional CBD synthase; and de Meijer et al. (2009) selected a variant of this that almost completely prevents the conversion of CBG into CBD.

The hypothesis that the enzymes that produce THCA (THCA synthase) and (CBDA CBDA synthase) from the same precursor compound, cannabigerolic acid, are controlled exclusively by two alleles of the same gene, was challenged recently by Weiblen et al. (2015). They found that THCA synthase and CBDA synthase are encoded by two separate but linked regions. THC-predominant plants simply have a non-functional copy of CBDA synthase, so they convert all cannabigerolic acid into THCA. Other evidence also indicates that other genes control the pathways to THCA and CBDA (Van Bakel et al. 2011; Onofri et al. 2015).

Regardless of the complexities of genic control of the cannabinoids, progeny of hybrids and backcrosses between marijuana (high-THC) and hemp (low-THC) parents segregate dramatically for THC production, so it should be possible to transfer desired characters. Accordingly, breeders should be allowed to employ high-THC germplasm for the purpose of producing low-THC cultivars.

## Cannabidiol harvest

The non-intoxicant cannabinoid CBD is considered to have an acceptable safety profile and considerable medicinal value (Iffland and Grotenhermen 2017), and in the last several years a large market demand has developed for the prescription pharmaceutical niche, and a considerable demand is also expected for over-the-counter preparations (Carus 2016). Indeed, huge investments are currently being made in CBD agronomics, despite the uncertain legal status of the industry (Gardner 2015/2016). Just as with THC and oilseed harvests, the architecture of the plants is an important determinant of productivity.

As noted below, cannabinoid extracts can be (and are) obtained from the foliage as well as from the reproductive parts of the plant. The inflorescences are far more concentrated in cannabinoids, but the foliage represents the largest biomass of the plants. In parallel with the earlier discussion of “dual purpose” industrial hemp being grown both for fibre and oilseed, *C. sativa* can be grown exclusively for extracted CBD, or as dual purpose plants grown for oilseed and CBD, as also discussed in the following.

Earlier, “marijuana” and “industrial hemp” were distinguished by THC content, marijuana developing high levels of THC and low levels (if any) of CBD, and vice versa for hemp. As noted in the following discussion, high-THC “marijuana” biotypes have been transformed into high-CBD biotypes, raising issues about their biological and legal classifications.

As also noted in the following, industrial hemp is being employed as a source of extracted cannabinoids (principally CBD), although such usage of "resin" is forbidden in some jurisdictions.

### Highless marijuana buds

For medicinal purposes, there is currently somewhat of a demand for so-called "highless marijuana"—a non-psychotropic herbal product that is high in CBD but low in THC, which can be smoked. Best known in this category is an Israeli CBD-rich, THC-poor strain called Avidekel. The market for highless marijuana in the form of "buds" exactly parallels the market for conventional intoxicating marijuana, but is much smaller, because most consumers of high-CBD products do not smoke or vaporize them, but prefer tinctures and edibles. The discussion previously presented regarding appropriate architecture for production of buds and the special suitability of indica type biotypes applies perfectly to highless marijuana, but it should be kept in mind that the market for this product is limited. There is a much larger interest in the production of CBD as an extract, as discussed next.

### High-resin biotypes

Aside from producing resin with considerable THC, marijuana biotypes produce much more resin than hemp cultivars (and so are referred to as "high-resin"). Marijuana plants have been modified by breeding to create biotypes that yield considerable CBD rather than THC. Elite lines of this class of plant are propagated by cuttings (exactly the method used for high-THC marijuana), but (unlike most high-THC marijuana) the plants are often being grown legally outdoors, since their abuse potential is limited. Because the biotypes represent intellectual property of considerable commercial value, information on their history is unavailable (the same is true for most commercial high-THC strains). Likely indica type strains were employed to a considerable extent as foundational parental material, since marijuana strains with considerable CBD as well as THC mostly belong to indica type, not sativa type. Certainly indica type plants represent ideal material for future breeding of high-CBD strains, for the reasons discussed in detail in this review.

In the marijuana trade, "trim" refers to leftover material of plants after the inflorescence has been harvested, usually for preparation of buds ("straw" is the usual term for waste material of crops). For purposes of extracting cannabinoids, the key portion of the trim is the foliage, not the twigs or stems. For CBD extraction, the trim from high-CBD strains has sold for over $1000 a pound or $2.20 a gram (O'Shaughnessy 2013). The CBD market has been estimated to have a value of $5 billion (Lee 2013). These figures explain the recent gold-rush mentality to develop the CBD industry. Because the foliage can be used as a source of CBD, the plants are often grown at very low density—1 or 2 plants per square metre (oilseed cultivars are grown at an average of about 125 plants per square metre)—in order to encourage branching and foliage development. The relatively low requirement for quantity of plants facilitates the use of planting stock based on cuttings or tissue propagation, which are much more expensive alternatives than employing conventional seeds. Of course, the uniformity of the plants produced is also advantageous. *Cannabis sativa* has probably been grown for at least 6000 years, and while it has been selected by humans for harvest of its stem and reproductive tissues, it has not been selected for harvest of foliage extracts. Tobacco may represent a model for judging criteria for this, although recent research on this crop has decreased dramatically.

### Low-resin biotypes

CBD can be salvaged from the straw remaining from the oilseed hemp harvest. Hempseed plants produce significantly smaller quantities of resin and cannabinoids (often by a factor of about five) than marijuana strains (the former are referred to as "low-resin"). Also contributing to a lower CBD yield, at the harvest stage for seeds much of the foliage is senescent and not ideal as a source of cannabinoids. However, by only harvesting the infrucescences, the seeds and remaining cannabinoid-rich straw can be easily separated, and the latter can be very high in CBD because of the very large presence of perigonal bracts (every seed is covered by a perigonal bract, which has grown considerably from the small bract covering the flower).

### Breeding for foliage harvest

The foliage of *C. sativa* is photosynthetically indispensable for production of all of the useful products discussed in this publication, but apart from its occasional use in southern Asia for production of weak intoxicating preparations, the leaves have usually been considered to be a waste product. With the recent explosion of interest in harvesting CBD and other non-euphoric cannabinoids from the foliage, the possibility may be considered of deliberately breeding for plants that produce high amounts of leaves. Such a possibility has not been seriously considered to date. However, as noted in Fig. 24, a high-foliage, low-THC cultivar has in fact been bred, although not for the purpose of harvesting the leaves. To allow maximum development of foliage, highly branched plants that are semi-dwarf in stature (since light cannot penentrate many layers of leaves) seem appropriate. Because the cannabinoids are produced in the epidermal secretory trichomes, it would be desirable to couple selection for overall form with selection for high concentrations of large secretory trichomes that are especially productive of resin.

## Summary of architectural ideotypes

The pork industry has a motto: “we use every part of the pig but the squeal” (the same has been said about hot dogs!). Uses also tend to be found for all parts of the world’s dominant crops, and it may be anticipated that with the increasing acceptance of *Cannabis sativa*, all of its constituents will find applications. However, as presented here, certain organs deserve emphasis for particular applications, and breeding for high productivity of these in appropriate field layouts is desirable. Figure 25 summarises the plant architectural types in relation to their most productive field configurations. Stem fibre has proven to be ideally produced from the unbranched stalk of very tall plants with minimal foliage, grown at very high density (Fig. 25A). By contrast, recent production of the cannabinoid CBD has been based to a considerable degree on the abundant foliage of short but extremely branched plants grown at very low density (Fig. 25E). However, the reproductive parts of the plant deserve the most emphasis. Seeds have traditionally been obtained from dual-purpose plants (also grown for fibre; Fig. 25B) and from highly branched, medium-height plants grown at low density (Fig. 25C), but it is now clear that semi-dwarf forms with limited

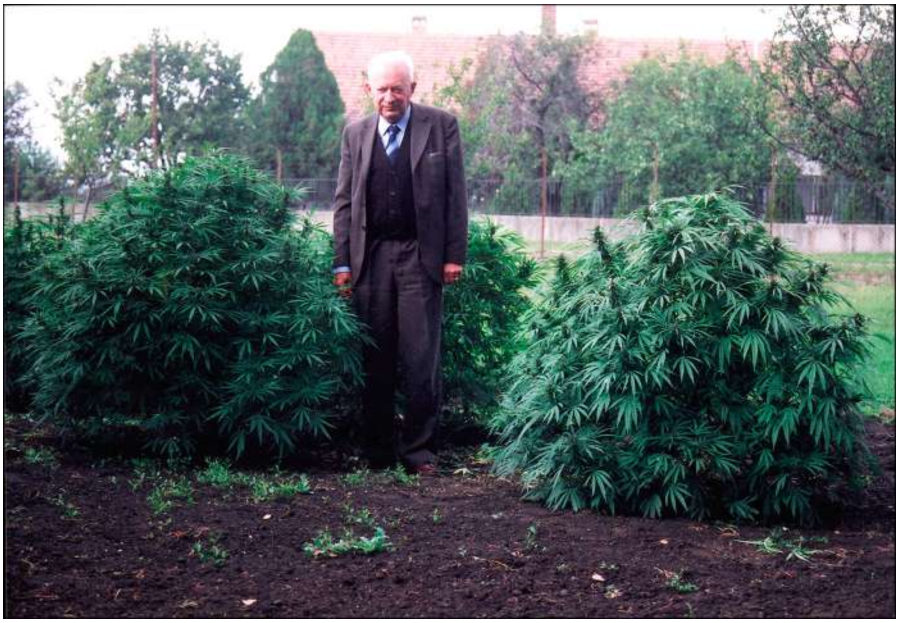


**Fig. 24** A high-foliage semi-dwarf biotype of *Cannabis sativa*, bred by the late Ivan Bócsa and registered as the cultivar ‘Panorama’ for use as an ornamental. Photo courtesy of Professor Bócsa

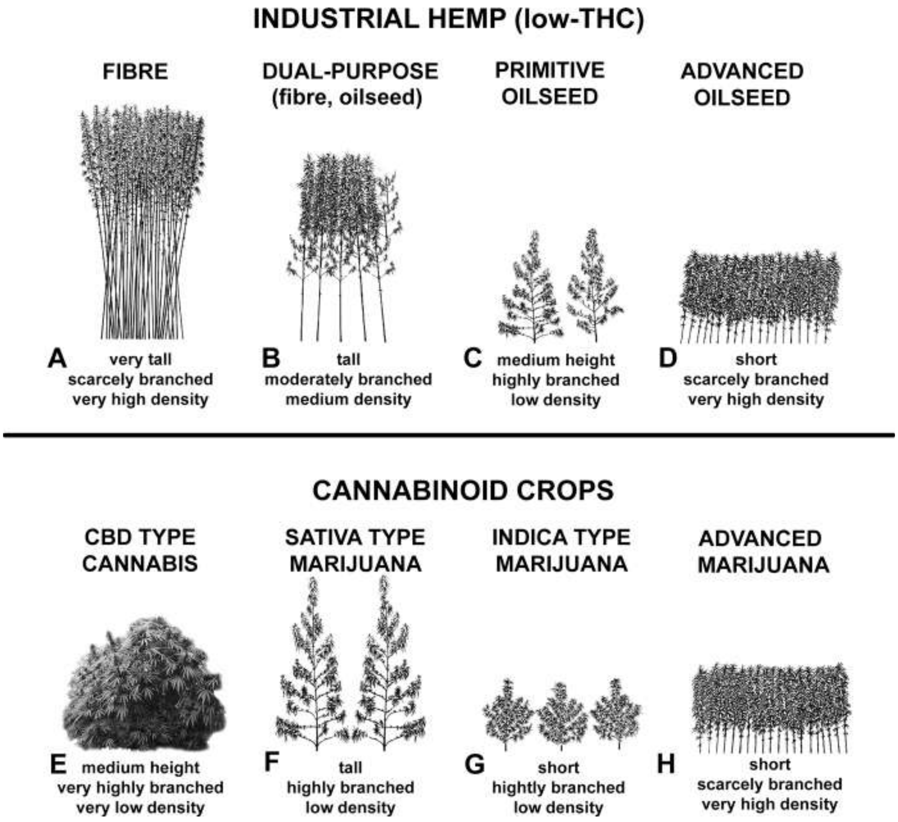


**Fig. 25** Summary of architectural ideotypes in field configurations. Prepared by B. Brookes

branching that are grown at very high density (Fig. 25D) represent the most efficient oilseed architecture. Cannabinoids (mostly THC) have been obtained from tall, branched plants (so-called "sativa type;" Fig. 25F) grown at low density, but the associated production of stems represents a huge wastage of energy. The ancient cultigen "indica type" marijuana (Fig. 25G), which is a semi-dwarf form, represents an excellent ideotype, but produces relatively small "buds" on its multiple branches. Unfortunately, as discussed previously, this category of plant is very difficult to find today. For indoor cultivation and to meet the market demand for very large buds, the advanced type of ideotype shown in Fig. 25H is ideal.

This paper has emphasized that dwarfing has proven to be a key strategy for increasing productivity of the world's major crops, and that this also represents the best tactic for breeding of efficient forms of *C. sativa*. As reviewed here, except for fibre production, decreasing height and in most cases also decreasing branching are appropriate strategies for oilseed and cannabinoid production. Four major classes of germplasm that can contribute to dwarfing have been identified here. Unfortunately, germplasm resources for *C. sativa* are quite unsatisfactory.

## The shamefully inadequate state of germplasm preservation of *Cannabis sativa*

As expressed by Watson and Clarke (1997): "The last 60–70 years have been disastrous for the *Cannabis* gene pool, and many local landraces, the result of hundreds of years of selection for local use, have been lost because of *Cannabis* eradication, neglect on the part of agricultural officials and industry, anti-*Cannabis* propaganda and the general trend (until recently) to reduce industrial hemp breeding and research." Welling et al. (2016) stated: "During the latter part of the twentieth century legitimate crop-types of *Cannabis*… not only failed to benefit from advances in breeding technologies and genetic resource utilization, but also suffered significant losses in ex situ conservation." International narcotics conventions have made legitimate collection and transfer of seeds a laborious and indeed extremely limited exercise, although illicit exchange has occurred very extensively. At present in North America, there are no conventional public genebanks from which one can obtain material for scientific study and technological development, or in which one can deposit valuable germplasm for potential long-term exploitation. Genebank resources for low-THC *C. sativa* are largely in a small number of European institutions and in China, and they are limited in extent and availability (Small 2016, chapter 17; Welling et al. 2016). Seeds for high-THC *C. sativa* can be purchased from commercial so-called "genebanks," but these are of uncertain status (they are almost always hybrids of unknown origin and of ambiguous or illicit legal standing). Marijuana seeds have been collected and even maintained by some national law enforcement agencies, but these are very rarely available for research or development, and are not being conserved according to the professional standards of genuine genebanks. It is curious indeed that at a time when scientific knowledge is generating spectacular technological advancements for the benefit of society, the narrow-minded prejudice and ignorance of some political leaders continue to hamper progress on a plant with enormous potential.

### Compliance with ethical standards

**Conflict of interest** The author declares that he has no conflict of interest.

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