On artificial F1-hybrids and backcrosses between *Taraxacum koksaghyz* and species of *Taraxacum* sect. *Taraxacum* (*T. officinale* s. l.) and their invasive potential

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Abstract: Uhlemann, I. & Thiele, K. 2024: On artificial F1-hybrids and backcrosses between *Taraxacum koksaghyz* and species of *Taraxacum* sect. *Taraxacum* (*T. officinale* s. l.) and their invasive potential. Schlechtendalia **41**: 1–16.

Taraxacum koksaghyz, a rubber producing plant grown in temperate regions, is used together with diploid *Taraxacum linearisquameum* (sexual *T. officinale* s. l.) or triploid species of *T.* sect. *Taraxacum* (agamospermous (micro-)species of *T. officinale* s. l.) as parental plants to get artificial rubber producing hybrids. *T. koksaghyz* × *T. oblongatum* and *T.* 'Hybrid 207' are extremely rare triploid offspring examples for 2×/3× combinations. The invasive potential of *T.* 'Hybrid 207' seems to be low, but interspecific competition with weeds is stronger than in *T. koksaghyz* which completely failed to compete against weeds. Artificial hybrids from 2×/2× combinations (*T. koksaghyz* × *T. linearisquameum* and reciprocal and backcrosses with parents) are diploid, generally have a morphological intermediate appearance between parents and partially produce rubber (0.1–3.7%). The fertility of achenes of offsprings depends on the parental function (pollen recipient or pollen donor). In case of *T. linearisquameum* as pollen recipient, fertility will be high (85–97%) and in case of *T. koksaghyz* as pollen recipient, fertility is low (1.5–9%).

Zusammenfassung: Uhlemann, I. & Thiele, K. 2024: Über künstliche F1-Hybriden und Rückkreuzungen zwischen *Taraxacum koksaghyz* und Arten von *Taraxacum* sect. *Taraxacum* (*T. officinale* s. l.) und deren invasives Potenzial. Schlechtendalia **41**: 1–16.

Taraxacum koksaghyz, eine Kautschuk produzierende potenzielle Kulturpflanze temperater Regionen, wird mit *T. linearisquameum* (sexuelles, diploides *T. officinale* s. l.) oder Arten der *T.* sect. *Taraxacum* (agamosperme, triploide (Klein-)arten von *T. officinale* s. l.) gekreuzt um künstliche, kautschukführende Hybriden zu erhalten. *T. koksaghyz* × *T. oblongatum* und *T.* ‚Hybride 207' sind sehr seltene triploide Kreuzungsprodukte von 2×/3× Kombinationen. Das invasive Potenzial der *T.* ‚Hybride 207' ist gering, aber das interspezifische Konkurrenzvermögen mit spontanen Unkräutern ist größer als bei *T. koksaghyz*, dessen Populationen innerhalb eines Jahres komplett zusammenbrechen. Künstliche Hybriden der 2×/2× Kreuzungen (*T. koksaghyz* × *T. linearisquameum*, oder reziprok oder Rückkreuzungen mit den Eltern) sind diploid, stehen morphologisch zwischen den Eltern und produzieren teilweise Kautschuk: 0,1–3,7 %. Die Fertilität der F1 hängt von der Verwendung der Eltern als Vater oder Mutter ab. Im Fall von *T. linearisquameum* als Mutter liegt die Fertilität bei 85–97%. Fungiert *T. koksaghyz* als Mutter liegt die Fertilität bei 1,5–9%.

Key words: Russian Dandelion, hybridization, spreading risk.

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Introduction

In most of the c. 60 sections of the cosmopolitan genus *Taraxacum*, coexistence of agamospermy and sexuality together with complex hybridity and polyploidy is common. In contrast to the tremendous infrageneric differentiation, only very few species are of commercial use and have the potential to become crops.

One of these few is the rubber producing *T. koksaghyz* (Russian Dandelion) from section *Ceratoidea* KIRSCHNER & ŠTĚPÁNEK (2008), which comprises about eight species (sexual or agamospermous) restricted to Central Asia, occurring on subsaline soil. The history of cultivation of Russian dandelion dates back to the first half of the last century, when Rodin (1933) discovered and described the species based on the "Verordnung über die Durchsicht der Flora der Union auf Kautschuk-führende Pflanzen" in the former Soviet Union. The capacity of this species was recognized easily and even one year later breeding and agronomic activities started in the Soviet Union, Ukraine, and Belarus (Ulmann 1951). At that time, undomesticated *T. koksaghyz* was cultivated on a large scale [1936: 5000 ha, 1938: 20000 ha, 1940: 65000 ha, 1941: 330000 ha] (Suomela 1950). Furthermore, European countries like Bulgaria (1943), Finland (1943), France (1943), Germany (1940), Great Britain (1943), Hungary (1943), Romania (1943), Spain and Sweden (1942) and even Australia and New Zealand (1942) started to grow Russian dandelion (Suomela 1950). From 1942 onwards, Canada and the USA followed (Whaley & Bowen 1947). However, these attempts soon declined, as Brazilian rubber (*Hevea brasiliensis*) was more readily available due to the removal of trade barriers caused by the war. The cultivation of *T. koksaghyz* as a rubber producer was recently resumed in various temperate regions,

such as Canada, China, Germany, The Netherlands, Kazakhstan, and the United States (Cherian et al. 2019, Cornish 2016, Gurao 2019, Uhlemann et al. 2019, van Beilen et al. 2007).

These activities lead to the question of gene flow between native species of the genus *Taraxacum* and cultivated *T. koksaghyz*. The potential of hybridization depends on the mode of reproduction, which can be obligate agamospermous (polyploid), facultative agamospermous (polyploid and diploid) or sexual (diploid). In Europe, many cytogeographical studies in the genus *Taraxacum* were carried out (e.g., Jenniskens et al. 1984, de Nijs et al. 1990, Uhlemann 2001) showing the distribution patterns of these reproductive systems. This is important for assessing the potential of gene flow in nature and recommending unproblematic locations for *T. koksaghyz* fields to avoid hybridization events.

There are two ways of reproductive interactions between *T. officinale* s. l. and *T. koksaghyz*. First, as pollen donor in case of an obligate agamospermous, triploid state of *T. officinale* s. l. ("micro"species of *Taraxacum* sect. *Taraxacum*) or, second, as both pollen donor or pollen recipient in the case of sexual *T. koksaghyz* and sexual *T. officinale* s. l. In the latter case, the sexual taxon is correctly and more precisely called *T. linearisquameum* (van Soest 1966) in terms of taxonomy and nomenclature using the oldest epitheton available for a sexual dandelion within the *T. officinale* complex.

The main research objective in this study is the production of artificial hybrids in controlled crosses between diploid, sexual parents (*T. linearisquameum* × *T. koksaghyz* and reziprocal and backcrosses) which successfully and readily produce fertile offspring. In addition to their character, complex detailed morphological descriptions, information on fertility and rubber content are given for the most promising hybrids.

Secondarily, attemps of controlled crosses between triploid, agamospermous species of *T.* sect. *Taraxacum* like *T. acervatulum*, *T. contractum*, *T. crassum*, *T. deltoidifrons*, *T. elegantius*, *T. oblongatum*, *T. pseudohabile*, *T. urbicola* as pollen donor and *T. koksaghyz* as pollen recipient nearly always failed to produce offspring (Uhlemann et al. 2019). Nevertheless, very rarely F1 hybrids were produced, and two cases are described here in detail. In addition, for one of these hybrids, experiments on interspecific competition and invasiveness were carried out.

Material and methods

T. koksaghyz (Tko) originally comes from a propagation population consisting of 14 *T. koksaghyz* accessions (Plant ID W6-35-156, -159, -160, -164, -166, -168, -169, -170, -172, -173, -176, -178, -181, -182) from Genbank (USDA) collected in 2008 during a research expedition by Barbara Hellier on classic sites of *T. koksaghyz*, in catchment area of rivers Kegen und Tekes in Kazakhstan (Hellier 2011).

T. linearisquameum (Tli) was collected in Austria, Vienna, district Brigitta, Brigittaplatz, lawn at church square, 14 Apr. 2017, I. Uhlemann (HAL 149939) (1); Austria, Vienna, district Brigitta, Brigittaplatz s, lawn between residential buildings, 18 Apr. 2017, I. Uhlemann (HAL 149938) (2); ibidem, 15 Apr. 2017, I. Uhlemann (HAL 149940) (3), (HAL 149941) (4).

T. oblongatum was collected from a spontaneous population growing on area of JKI Quedlinburg in spring 2018. Seeds from the original plant are kept in the Dandelion working group of the JKI Quedlinburg.

***T.* '*Hybrid 207*'** originates from crossbreeding experiments done by F. Eickmeyer (ESKUSA, Parkstetten) in 2012. This hybrid is an offspring result from *T. koksaghyz* (pollen recipient) and *T. officinale* **'**RT breeding line' (ESKUSA GmbH) as pollen donor (mentioned under the name *T. officinale* "Riesentreib" in Uhlemann et al. (2019). **'**RT breeding line' cannot be assigned to any described (agamo-)species within *T.* sect. *Taraxacum* (*T. officinale* s. l.). Superficially, it resembles *T. ekmanii* with regard to robust and large habit, a few broad and dentate broad triangular lateral lobes, recurved to reflexed unbordered outer bracts and dark stigmata.

Parental crossbreeding experiments were carried out in ten combinations to produce F1:

01 - *Taraxacum linearisquameum* (Vienna 1) × *Taraxacum koksaghyz*, Origin: JKI, 2018
02 - *Taraxacum linearisquameum* (Vienna 2) × *Taraxacum koksaghyz*, Origin: JKI, 2018
03 - *Taraxacum linearisquameum* (Vienna 3) × *Taraxacum koksaghyz*, Origin: JKI, 2018
04 - *Taraxacum linearisquameum* (Vienna 4) × *Taraxacum koksaghyz*, Origin: JKI, 2018

05 - *Taraxacum koksaghyz* × *Taraxacum linearisquameum* (Vienna 1), Origin: JKI, 2018
06 - *Taraxacum koksaghyz* × *Taraxacum linearisquameum* (Vienna 2), Origin: JKI, 2018
07 - *Taraxacum koksaghyz* × *Taraxacum linearisquameum* (Vienna 3), Origin: JKI, 2018
08 - *Taraxacum koksaghyz* × *Taraxacum linearisquameum* (Vienna 4), Origin: JKI, 2018
09 - *T. koksaghyz* × *T. oblongatum*, Origin: JKI, 2018
10 - *T. koksaghyz* × *T. officinale* **'**RT breeding line' = 'Hybrid 207', Origin: F. Eickmeyer (ESKUSA (Parkstetten, Germany) 2012.

Backcrossbreeding experiments were carried out in six combinations (F1 x Parents):

11 - *T. koksaghyz* × (*T. koksaghyz* × *Taraxacum linearisquameum* (Vienna 2)), Origin: JKI, 2020.
12 – (*T. koksaghyz* × *Taraxacum linearisquameum* (Vienna 2)) × *T. koksaghyz*, Origin: JKI, 2020.
13 - *T. koksaghyz* × (*T. koksaghyz* × *Taraxacum linearisquameum* (Vienna 1)), Origin: JKI, 2020.
14 - (*T. koksaghyz* × *Taraxacum linearisquameum* (Vienna 1)) × *T. koksaghyz*, Origin: JKI, 2020.
15 - (*T. linearisquameum* (Vienna 1) × *T. koksaghyz*) × *T. koksaghyz*, Origin: JKI, 2020.
16 – *T. koksaghyz* × (*T. linearisquameum* (Vienna 1) × *T. koksaghyz*), Origin: JKI, 2020.

Controlled crosses

Controlled crosses were carried out between *T. koksaghyz* and *T. linearisquameum* and reziproke (F1), between F1 and parents (backcrosses), as well as between *T. koksaghyz* and *T. oblongatum*. After anthesis, two capitulae of each crossing partner were brought together for a few seconds in a circular motion under insect-free conditions in the greenhouse. The pollinated capitulae matured for about three weeks on the mother plant, and subsequently the ripe seeds of each were collected in bags (each for one capitulum).

Monitoring of inter- and intraspecific competition

651 plants of *Taraxacum* 'Hybrid 207' were planted in agricultural fields in six rows with 50 cm between them, free from weeds. These experimental (succession) fields were subsequently colonised by native plants (mainly weeds). Releves were carried out monthly according to Braun Blanquet (1964) to analyze the competitive ability of *Taraxacum* 'Hybrid 207' in natural vegetation. The monitoring period was from April to September 2018 und from April to July 2019.

Determination of rubber content

Roots were harvested, dried to constant weight at 60 °C and grinded in a powder mill. An aliquot of 100 mg was measured by NMR spectroscopy at lifespin GmbH (Regensburg, Germany) (STOLZE et al. 2017).

Determination of chromosome numbers

The squash method was applied to the root tips of seedlings, which were pre-treated with 0.002 M 8-hydroxyquinoline (4 h), Carnoy fixative (12 h), hydrolyzed in 1 M HCL (5 min, 60 °C) and stained with aceto-carmine to determine the chromosome number. The reproductive system (agamospermy versus sexuality) in *Taraxacum* can be determined by the number of chromosomes. Diploid taxa (2n = 2× = 16) are sexual and taxa with triploid or higher level (2n = 3× = 24 or higher level) are agamospermous (De Nijs et al. 1990). The determination of ploidy level was additionally done by flow cytometry by Christian Schulze Gronover (Fraunhofer IME, Münster), according a standard plant cell protocol (Mártonfiová 2015).

Results

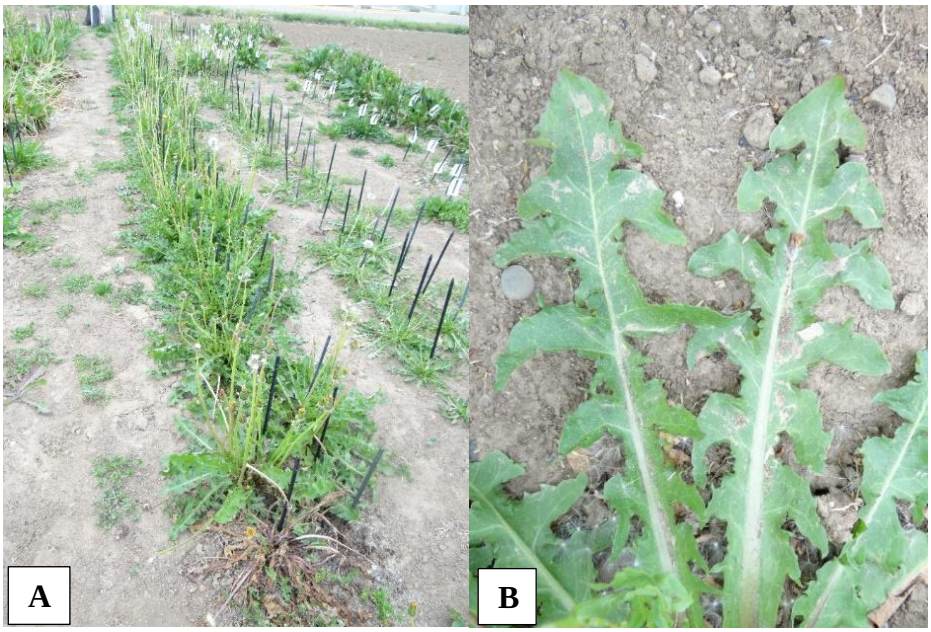
I Crosses of *T. koksaghyz* (diploid, sexual, pollen recipient) and *T. oblongtum / T. officinale* 'RT breeding line' (triploid, agamospermous, pollen donor)

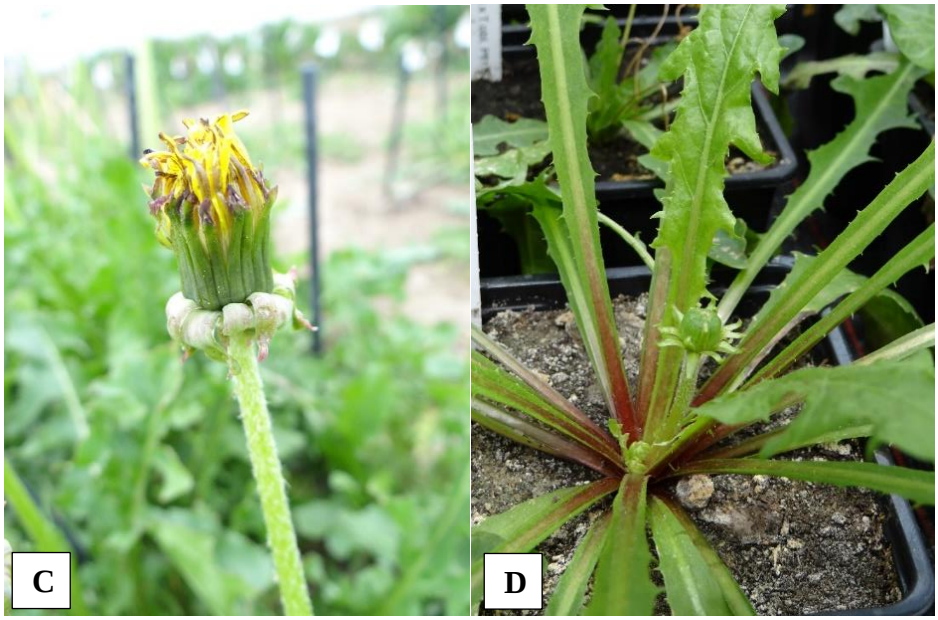
T. koksaghyz* × *T. oblongatum (**Fig. 1)**
In spring 2018, after artificial crossing of both species only one seed out of 25 fertile seeds developed into a plant morphologically intermediate between parents having an agamospermous mode of reproduction. The remaining 24 fertile seeds developed to *T. koksaghyz* probably due to self-fertilising caused by mentor effect due to *T. oblongatum* pollen.

Original material: *T. koksaghyz* × *T. oblongatum*, Origin: JKI, 22.5.2020 (HAL 158844)

Description:

Plant 25–30 cm tall, robust. **Leaves** subsucculent, patent to suberect, bluish green, glabrous, not spotted, pinnatisect, terminal lobe triangular to subcordate, sometimes with a short lingulate tip, lateral margins entire, dentate or contracted; lateral lobes 4–5 pairs, recurved to hamate, broad triangular, distal margin convex, dentate, proximal margin ±straight to concave, dentate; interlobes distinct, crispate, green, dentate; petiole winged, purple, midrib green or brownish green. **Scapes** green, subglabrous. **Capitulum** c. 40 mm in diameter, yellow; outer ligules flat, striped grey-purple abaxially; styles in the upper part light grey abaxially; pollen present, pollen grains irregular in diameter. **Involucre** olive-green, slightly pruinose; **exterior bracts** 14–15, recurved to reflexed with a small white border, with corniculations below the apex, adaxially white-greyish suffused with pink, abaxially dark green, (3–)4–6 mm wide, (11–)12–13 mm long. **Achenes** dark grey, achene body 3.0–3.3 mm long, coarsely spinulose in the upper part, abruptly narrowing into a 1.0–1.1(–1.5) mm long cylindrical cone; rostrum 8.5–9.8 mm long; pappus white.





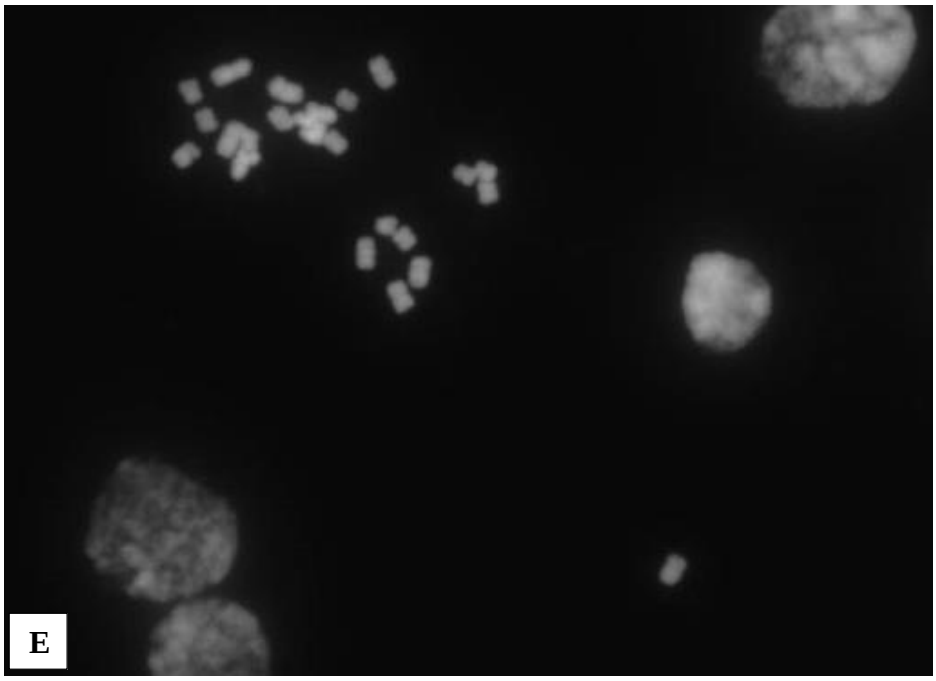


Fig. 1: *T. koksaghyz* × *T. oblongatum*, Julius Kühn Institute (JKI), Quedlinburg, field; 22 May 2020, I. Uhlemann: A – view to plot with agamospermous generated F1 plants of the original hybrid; B – leaves. JKI Quedlinburg, greenhouse, 1.7.2018, I. Uhlemann: C – capitulum; D – single hybrid plant in an early stage of development. E – Mitotic metaphase plate of root tips.

Annotation: The robustness of the morphologically intermediate plant, leaf lamina with large distinct recurved to hamate lateral lobes and recurved to reflexed outer bracts point to *T. oblongatum* (father) whereas corniculations on tips of bordered outer bracts, achenes with long cylindrical cone and subsucculent leaf consistence are characters similar to *T. koksaghyz* (mother).

Fertility: 10 capitulae were analysed. The number of achenes per capitulum is (85–)130–159 (average: 124.4). The percentage of fertile achenes per capitulum varies between 78.5 and 93.3% (average: 80.8%).

Ploidy level: 2n=3×=24 (Fig. 1E).

T. 'Hybrid 207' (*T. koksaghyz* × *T. officinale* 'RT breeding line', Eskusa GmbH) (Fig. 2)

Original material: *T. koksaghyz* × *T. officinale* 'RT breeding line' = 'Hybrid 207': JKI, 23 Apr. 2018 (HAL 141327)

Description:

Plant c. 20 cm tall, robust. **Leaves** erect to subpatent, subsucculent, green, glabrous, not spotted, pinnatisect, terminal lobe triangular, longer than wide, lateral margins dentate; lateral lobes 3–4 pairs, ± patent, broad triangular, distal margin straight to convex, entire or more often with one or few big teeth, proximal margin convex, entire; interlobes short, green; petiole winged, green, midrib green or brownish green. **Scapes** brownish green, aranose below involucre. **Capitulum** c. 40 mm in diameter, yellow; outer ligules flat, striped dark grey-purple abaxially; styles in the upper part dark grey abaxially; pollen present, pollen grains irregular in diameter. **Involucre** dark green, not pruinose; **exterior bracts** 12, erecto-patent to slightly recurved, tips bend upwards, with a distinct white border, with corniculations below the apex, adaxially white-greyish, tips sometimes reddish, abaxially dark green in the median part, greyish green laterally, 4–5 mm wide, 13–16 mm long. **Achenes** pale grey, achene body 3.1–3.3 mm long, spinulose in the upper part, abruptly narrowing into 0.8–1.0 mm long (sub-)cylindrical cone; rostrum 7.0–7.2 mm long; pappus white.

Annotation: *T.* 'Hybrid 207' is morphologically intermediate between parents. *T. koksaghyz* characters (mother) are well-developed appearing in an intermediate leaf and capitulum morphology. Leaves are slightly succulent but have in contrast to *T. koksaghyz* a complex lobation pattern; outer

bracts have a distinct white border, well-developed coniculations and more or less patent position. Due to its short rostrum in particular achenes, it tends to those of *T. koksaghyz.* With its *T. officinale* father *T.* 'Hybrid 207' shares a strong susceptibility for powdery mildew.

Fertility: 16 capitulae were analysed. The number of achenes per capitulum varies between 91 to 116 (average: 102.6). The percentage of fertile achenes per capitulum varies between 36.0 and 68.1 % (average: 56.3%).

Ploidy level: 2n=3x=24.

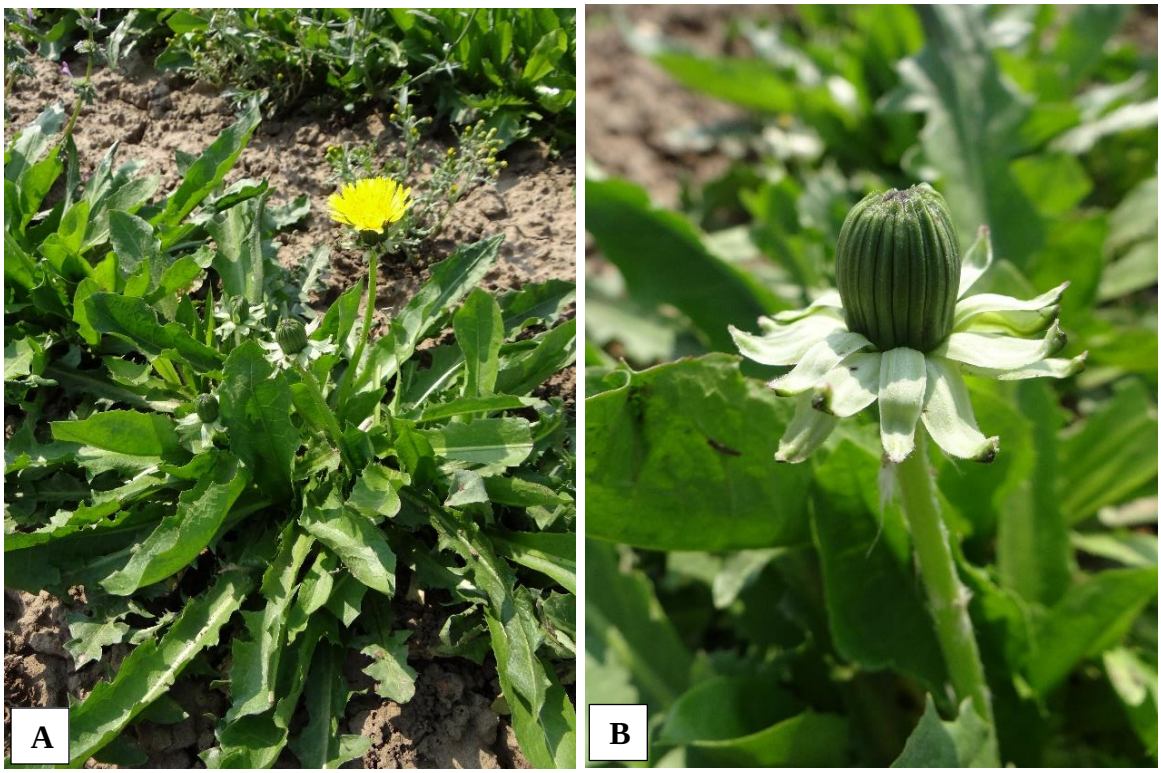


Fig. 2: *T.* ´Hybrid 207´, Julius Kühn Institute (JKI), Quedlinburg; A – habit, B – capitulum 23 Apr. 2018, I. Uhlemann.

Interspecific competition and invasive potential

Table 1 and Fig. 3 show *Taraxacum* 'Hybrid 207' in succession plots adjacent to fields (*Phacelia tanacetifolia*) of Julius Kühn Institute Quedlinburg subsequently colonised by native herbs (weeds). In April 2018, when monitoring started, *Taraxacum* 'Hybrid 207' dominated the plot with about 40% covering and was accompanied by nine native herbs with relatively low covering. Both the number of native species and their covering increased (May–July 2018) and subsequently decreased (August–September 2018) slightly. In spring 2019, the covering was similar as in 2018, but later (July) *Phacelia tanacetifolia* from adjacent fields aggressively colonised the plot and finally dominated.

The initial number of 651 plants of *Taraxacum* 'Hybrid 207' decreased within the first year to 447 plants, presumably due to intraspecific competition. In summer 2019, c. 350 plants survived, a decline of 46.2%.

The invasive potential of *Taraxacum* 'Hybrid 207' seems to be extremely low. While *T. koksaghyz* populations spread readily within the plot and covered the spaces between rows readily within few months, in *Taraxacum* 'Hybrid 207' such a tendency was not documented, neither within the plot between the rows nor in the vicinity of the plot any additional plants were observed.

Table 1: *Taraxacum* 'Hybrid 207' succession adjacent to fields of Julius Kühn Institute Quedlinburg; six rows with 50 cm between. Monitoring period: April-September 2018 and April-July 2019.

number	1	2	3	4	5	6	7	8
date	21.04. 2018	21.05. 2018	01.07. 2018	04.08. 2018	22.09. 2018	06.04. 2019	27.04. 2019	01.07. 2019
field area [m²]	18	18	18	18	18	18	18	18
total cover [%]	70	85	90	65	30	80	90	95
number of native species	09	13	11	07	07	09	10	09
Taraxacum 'Hybrid 207' cover	4	4	5	4	2	4	4	2
Taraxacum 'Hybrid 207' plants	651	590	533	458	447	399	383	c. 350
Stellarietea mediae-species								
Capsella bursa-pastoris	+	+	·	·	·	+	1	+
Cirsium arvense	+	+	+	+	+	·	r	+
Galium aparine	·	r	r	·	·	1	1	1
Lamium amplexicaule	1	r	·	·	·	+	+	·
Senecio vulgaris	+	+	·	·	·	+	+	·
Solanum nigrum	·	+	r	r	r	·	·	·
Sonchus asper	·	·	r	r	·	+	+	·
Stellaria media	2	+	+	·	·	+	+	+
Thlaspi arvense	r	+	·	·	·	·	·	·
Urtica urens	r	r	r	·	·	·	·	·
Sisymbrietea-species								
Chenopodium album	·	r	r	r	r	·	·	·
Conyza canadensis	·	+	+	+	+	+	+	+
Lactuca serriola	·	·	r	·	·	·	·	r
Matricaria recutica	r	r	·	·	·	·	·	+
Phacelia tanacetifolia	r	1	1	1	1	1	2	4
Picris hieracoides	·	·	r	r	r	·	·	·
Molino-Arrhenatheretea-species								
Taraxacum officinale	·	·	·	·	r	+	+	r

Fig. 3: Phenology of a *Taraxacum* – 'Hybrid 207' – plot within agricultural land of the Julius Kühn Institute, Quedlinburg. Upper row: 21 May 2018, lower row: 27 Apr. 2019.

II Crosses of *T. linearisquameum* (diploid, sexual) and *T. koksaghyz* (diploid, sexual)

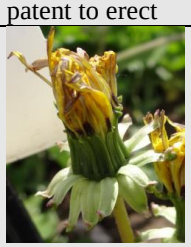
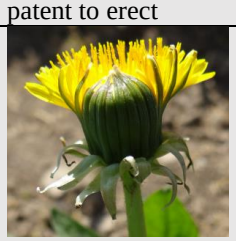
In order to produce fertile offspring, *T. linearisquameum* as a sexual crossing partner was chosen for *T. koksaghyz*. The material was collected on classical sites in Vienna (Austria), where at first diploid, sexual plants of common dandelion were studied intensively (Fürnkranz 1960, Tschermak-Woess 1949). In Table 2 relevant characters of parents and F1 (hybrids) are listed.

In general, hybrids have an intermediate morphological appearance between parents. Nevertheless, qualitative *T. koksaghyz* characters are the succulence of leaves and corniculations (horns) on tips of bordered outer bracts, whereas typical *T. linearisquameum* characters are the robust habit and a well differentiated leaf-lobation pattern. Further morphological characters are developed proportionately, i.e., formed in a more or less fifty-fifty proportion, like position of outer bracts, which is usually more or less patent, and length of rostrum of achene. Interestingly, one character clearly depends on parental function (pollen recipient or pollen donor): the fertility of achenes. When *T. linearisquameum* is pollen recipient, fertility will be high (85–97%) and when *T. koksaghyz* is pollen recipient, fertility will be low (1.5–9%).

In Table 3, all crossbreeding results are listed. Offspring varies morphologically within limits outlined in Table 2. The most promising offspring regarding rubber content was produced by *T. koksaghyz* × *T.*

linearisquameum (Vienna 4), origin: JKI, 2018, varying from 1.4–3.7%. This hybrid and for comparison the reciprocal crossing are described and pictured afterwards in more detail.

Table 2: Main morphological differences between *T. koksaghyz*, *T. linearisquameum*, and hybrid offspring (compare also Figs: 4–5)

Characters		*T. koksaghyz*	Hybrids		*T. linearisquameum*
			T. koksaghyz (♀) × *T. linearisquameum* (♂)	*T. linearisquameum* (♀) × *T. koksaghyz* (♂)	
Leaf	consistency	subsucculent	subsucculent	subsucculent	not succulent
	colouration	glaucous grey-green	glaucous grey-green	mid green or greyish green	mid green or greyish green
	Lobe shape	missing or short triangular, obtuse	present, long triangular or lacinate	present, long triangular or lacinate	present, long triangular or lacinate
Involucre	Outer bracts position	erect to adpressed	(slightly recurved) to patent to erect	slightly recurved to patent to erect	recurved
					
	Inner bracts length	10–13 mm	(12–)14–17 mm	(13–)17–19 mm	13–18 mm
	Outer bracts length	7–10 mm	(8–)9–12(–13) mm	(8–)11–12(–16) mm	10–12 mm
	Outer bracts width	1–2 mm	(2.0–)4–5(–6.0) mm	(2.0–)3.0–4.0(–6.5) mm	1.5–2.5 mm
	Outer bracts horns	Well-developed	developed or absent	developed	absent
Achene	Total length	2.8–3.8 mm	(2.8–)3.8–4.2 mm	3.5–4.0 mm	3.0–3.7 mm
	Cone length	(0.5–)0.7–1.0 mm	0.8–1.1 mm	(0.3–)0.5–0.7(–1.0) mm	0.3–1.0 mm
	Cone shape	subcylindric-cylindric	subcylindric-cylindric	conic-cylindric	subcylindric-cylindric
	Rostrum length	3.0–5.0 mm	(3–)4.0–5.0(–7.0) mm	(4–)5–6(–7.5) mm	(8–)9.5–11 mm
Ligule	Stigma colour	pure yellow	yellow-light grey-grey-dark grey-blackish	yellow-light grey-grey-dark grey-blackish	Greyish green
	Pollen size	regular	regular	regular	regular
Chromosome number		2n = 16	2n=16	2n=16	2n= 16
Reproduction		sexual	sexual	sexual	sexual

***T. koksaghyz* × *T. linearisquameum* (Vienna 4) (Fig. 4)**

The offspring comprises **16** plants. **15** plants have an intermediate character between parents. One plant is *T. koksaghyz*.

Original material: *Taraxacum koksaghyz* × *T. linearisquameum* (Vienna 4). Origin: JKI, 6 Apr. 2019 (HAL 141048)

Description:

Plant 15–20 cm tall, robust. **Leaves** subsucculent, patent to suberect, bluish green, glabrous, not spotted, pinnatisect, terminal lobe triangular to helm-shaped, often with a short lingulate tip, lateral margins entire; lateral lobes 5–6 pairs, patent to slightly recurved to hamate, broad triangular, distal margin convex, entire or with small teeth, proximal margin ± straight to concave, entire; interlobes distinct but short, green; petiole winged, green, midrib green or brownish green. **Scapes** green, intensely aranose in particular below involucre. **Capitulum** c. 40 mm in diameter, yellow; outer ligules flat, striped grey-purple abaxially; styles in the upper part light grey abaxially; pollen present, pollen grains are regular in diameter. **Involucre** olive-green, not pruinose; **exterior bracts** 13, erect to patent, with a wide white border, with corniculations below the apex, adaxially white-greyish, abaxially dark green, (2.5–)3–5(–6.5) mm wide, (11–)12–14 mm long. **Achenes** grey, achene body 3.0–3.2 mm long, coarsly spinulose in the upper part, abruptly narrowing into a 1.0 mm long cylindrical cone; rostrum 7 mm long; pappus white.

Annotation: The offspring is in general intermediate between parents but tends habitually more to *T. koksaghyz* (mother) and is closer to it than in other hybrids, which is also confirmed by its high rubber content. *T. koksaghyz* characters appear in an intermediate leaf and capitulum morphology. Leaves are bluish green, slightly succulent with a simple but distinct lobation pattern; outer bracts have a wide distinct white border, well developed coniculations and an erect position and achenes have a long cylindrical cone and a relatively short rostrum. For its morphological similarity to reciprocal crossing, see description of and comments to the next hybrid.

Rubber content: 1.4–3.7 %, average: 2.3 %. 5 plants were tested. It is the highest rubber content observed in all hybrids, even as high as in some *T. koksaghyz* types.

Ploidy level: 2n=2×=16.

Fig. 4: *T. koksaghyz* × *T. linearisquameum* (Vienna 4), Julius Kühn Institute (JKI), Quedlinburg; 6 Apr. 2019, I. Uhlemann; A – view to plot; B – capitulum.

***T. linearisquameum* (Vienna 4) × *T. koksaghyz* (Fig. 5)**

The offspring comprises **23** plants of intermediate character between parents.

Original material: *T. linearisquameum* (Vienna 4) × *T. koksaghyz*. Origin: JKI, 6.4.2019 (HAL 158867)

Description:

Plant 15–20 cm tall, robust. **Leaves** subsucculent, patent to suberect, bluish green, glabrous, not spotted, pinnatisect, terminal lobe triangular to helm-shaped, often with a short lingulate tip, lateral margins convex, entire; lateral lobes 5–6 pairs, patent to slightly recurved sometimes broad lingulate, broad triangular, distal margin convex, entire or with small teeth, proximal margin ± straight to convex, entire or with a few small teeth; interlobes distinct, short, green; petiole winged, green, midrib green or brownish green. **Scapes** green, intensely aranose in particular below involucre. **Capitulum** 40–43 mm in diameter, yellow; outer ligules flat, striped grey-purple abaxially; styles in the upper part light grey abaxially; pollen present, pollen grains are regular in diameter. Involucre olive-green, not pruinose; **exterior bracts** 13–15, patent, with a small but distinct white border, with corniculations below the apex, adaxially white-greyish, abaxially dark green, (2.0–)3–4(–6.5) mm wide, (8–)10–14(–16) mm long. **Achenes** grey, achene body 3.0 mm long, coarsly spinulose in the upper part, abruptly narrowing into a 1.0 mm long cylindrical cone; rostrum 6 mm long; pappus white.

Annotation: The offspring basically is intermediate between parents but tends habitually more to *T. koksaghyz* (father). *T. koksaghyz* characters are well-developed, visible in an intermediate leaf and capitulum morphology. Leaves are bluish green, slightly succulent with a simple but distinct lobation pattern; outer bracts have a small but distinct white border, well-developed corniculations and a patent to suberect position; achenes have an abrupt transition into a long cylindrical cone and a relatively short rostrum.

This crossing and the reciprocal one are morphologically extremely similar, which is unique among all combinations tested. In general, offspring tends more to mother, but in the present case, when *T. linearisquameum* is the mother, the offspring is intermediate between the parents, and it is distinguished from the former hybrid only by a smaller white border on the outer bracts. Even the rubber content is relatively high.

Rubber content: 1.2–2.8%, average: 1.8%. 9 plants were tested.

Ploidy level: 2n=2x=16.

Fig. 5: *T. linearisquameum* (Vienna 4) × *T. koksaghyz*, Julius Kühn Institute (JKI), Quedlinburg; 6.4.2019, I. Uhlemann; A – view to plot; B – capitulum.

Table 3: Offspring characters (F1) of eight cross-combinations between diploid, sexual *T. linearisquameum* (Tli) and diploid, sexual *T. koksaghyz* (Tko). Rubber content of a comparable population of Tko is 3.66% ± 2.06% with a variation between 1.4 and 9.1%. In Tli rubber content is 0.21% ± 0.09%, whereas 0.1% is the detection limit for this method.

	No.	1	2	3	4	5	6	7	8
		Crossing				Reciprocal crossing			
Parents	Pollen recipient	Tli1	Tli2	Tli3	Tli4	Tko	Tko	Tko	Tko
	Pollen donor	Tko	Tko	Tko	Tko	Tli1	Tli2	Tli3	Tli4
Offspring	total	20	15	129	23	30	25	42	16
	Tli self	19	-	-	-	-	-	-	-
	Tko self	-	-	-	-	12	-	-	1
	hybrid Tko/Tli	1	15	129	23	18	25	42	15
Achens number	Total	200	272	177	137	151	131	163	136
	sterile	19	8	7	20	138	125	155	134
	fertile	181	264	170	117	13	6	8	2
	fertile [%]	91 %	97%	96%	85%	9%	5%	5%	1.5%
Morphology	Outer bracts border	**small**	**small**	absent	**small**	**small**	**small**	**small**	**wide**
	Outer bracts corniculation	**present**	absent	absent	**present**	**present**	**present**	**present**	**present**
	Outer bracts position	patent	slightly recurved	slightly recurved	patent	patent	erect	patent	erect to patent
	achene cone length [mm]	0.3–0.5	0.5	0.7	**1.0**	**0.8–0.9**	**1.0–1.1**	**0.8**	**1.0**
	body-cone transition	abrupt	abrupt	**gradual**	abrupt	**gradual**	abrupt	abrupt	abrupt
	rostrum length [mm]	**(4–)5–7**	6.5	7.5	6	**4–5**	**4**	**3**	7
	general	interm.	< Tli	< Tli	< Tko	< Tko	< Tko	< Tko	< Tko
Rubber content [%]	variation	0.1–0.3	not done	0.1–1.5	1.2–2.8	0.5–1.5	not done	0.7–1.6	1.4–3.7
	average	0.2	not done	0.4	1.8	0.9	not done	1.1	2.3
	testet plants	4	not done	10	9	10	not done	9	5

Abbreviations: Offspring: Tli self: selfcrossing of Tli due to the mentor pollen effect; **Tko self**: selfcrossing of Tko due to the mentor pollen effect; **Achenes number**: total, sterile and fertile number of achenes is average from 5 capitulae counted; **Morphology:** general morphology (general): closer to Tko (< Tko), closer to Tli (< Tli), intermediate (intermed). **Bold printed** characters indicate *Taraxacum koksaghyz* features.

III Backcrosses of F1 with *T. linearisquameum* or *T. koksaghyz*

This series of artificial hybrids was produced in 2020 and flowered for the first time in spring 2021. Out of six controlled backcrosses, four (11–14) are close to *T. koksaghyz* deviating from this species only in a sometimes more vigorous habit and few quantitative characters like outer bracts position and achene morphology. One of them is described here in detail. The rubber content varies from (0.35–)0.85–3.39%.

Further two (15–16) controlled backcrosses produced plants of intermediate appearance between parents similar to ‘Hybrid 207’.

The rubber content is relatively low and varies from 0.15–1.18%.

***T. koksaghyz* × (*T. koksaghyz* × *T. linearisquameum*, Vienna 2) (Fig. 6)**
The offspring comprises 18 plants morphologically close to *T. koksaghyz*.

Original material: *T. koksaghyz* × (*T. koksaghyz* × *T. linearisquameum*, Vienna 2). Origin: JKI, 13.6.2021 (HAL 158842)

Description:

Plant 15–20 cm tall, subrobust. **Leaves** subsucculent, bluish-green, glabrous, not spotted, pinnatisect, terminal lobe triangular, often with a short lingulate tip, lateral margins convex, entire; lateral lobes 5 pairs, patent to slightly recurved, broad triangular, distal margin convex, entire or provided with a few minute teeth, proximal margin ± straight, entire; interlobes distinct and well-developed, green; petiole unwinged, green, midrib green. **Scapes** green, aranose below involucre. **Capitulum** 15–20 mm in diameter, yellow; outer ligules flat, striped grey-purple abaxially; styles in the upper part grey abaxially; pollen present, pollen grains regular in diameter. **Involucre** light green, not pruinose; **exterior bracts** 14–15, erect, with a distinct white or pinkish border, with large corniculations below the apex, adaxially and abaxially light green, (1.5–)2(–3) mm wide, 9–11 mm long. **Achenes** grey, achene body 2.8–3.0 mm long, spinulose in the upper part, abruptly narrowing into a 1.0 mm long subcylindrical cone; rostrum 5–6 mm long; pappus white.

Annotation: The offspring is very close to *T. koksaghyz*. It deviates from this species in a more vigorous habit, pinnatisect leaves, erect outer bracts, achens with a little bit longer rostrum, an abruptly inserted pyramide and grey styles on ligules.

Rubber content: 1.17–1.43 %, average: 1.31%. Three plants were tested.

Fig. 6: *T. koksaghyz* × (*T. koksaghyz* × *T. linearisquameum*, Vienna 2), Julius Kühn Institute (JKI), Quedlinburg; 13 June 2021, I. Uhlemann. Left: Hybrid. Right: *T. koksaghyz*.

Discussion

Hybridization potential of diploid × triploid hybrids

The results demonstrate that true hybridization events between triploid agamospermous species of *T.* sect. *Taraxacum* and sexual *T. koksaghyz* under experimental conditions are rare. Out of c. 50 controlled crosses between *T. oblongatum* and *T. koksaghyz* in total only 25 fertile seeds were produced from which only one single seed developed into a true hybrid. Further attempts of controlled crosses including eight triploid agamospecies as pollen donors completely failed to produce offspring (Uhlemann et al. 2019). Similar results were reported by Poddubnaja-Arnoldi (1939a,b), Josefsson (1952), Fürnkranz (1960) and Černý et al. (2010). The main reason for low offspring percentages probably is the unavailability of fertile pollen in triploid agamosperm *Taraxacum* plants, which is caused by irregular and unbalanced meiosis (Małecka 1965). Furthermore, Małecka (1971) studied supposed spontaneous hybrids between *T. koksaghyz* and *T. officinale* in the botanical garden in Jena (Germany). Both parents were proven to be triploid and the supposed offspring (morphological intermediate plants in the vicinity of parents) was hypertriploid.

However, the triploid cytotype, morphological characters provided and a photo of the supposed *T. koksaghyz* specimen (Małecka 1971: 180 f., fig. 20) lead to reasonable doubts as to the correct interpretation of the material. This is supported by the finding of Kirschner et al. (2013) that most germplasm accessions assigned to *T. koksaghyz* truly belong to *T. brevicorniculatum*. Low percentages of seed set and germination rate in putative hybrids, in particular under natural conditions, were also mentioned in studies carried out in the USA by Iaffaldano et al. (2018), which lead to the assumption of a hybridization rate of 1:100000. The fertility of seeds considered in this study varies considerably and ranges from 56.3% (36.0–68.1%) in 'Hybrid 207' and to 80.8% (78.5–93.3%) in *T. koksaghyz* × *T. oblongatum*. In both hybrids, triploidy was proven by mitotic metaphase plates and irregular pollen grains diameter – two facts which reliably indicate agamospermous mode of reproduction, which normally leads to a higher percentage of fertile achenes. As a possible explanation, facultative agamospermy should be taken into account as Jenniskens et al. (1984) had mentioned for some populations of native Taraxaca in Southern Germany.

Diploid × diploid hybrids

In contrast to crosses between species of different ploidy levels, the combination of sexual diploids (*T. linearisquameum* × *T. koksaghyz* and reciprocal and backcrosses) easily produced viable hybrids, as already Fürnkranz (1960) and Iaffaldano et al. (2018) stated. On the other hand, the percentage of fertility of seeds in hybrids depends on parental function (pollen recipient or pollen donor). In case of *T. linearisquameum* as pollen recipient, fertility will be high (85–97%) and when *T. koksaghyz* is pollen recipient, fertility will be low (1.5–9%) as observed in our study. To comprehend the reason for this phenomenon, further studies are required.

Invasive potential and interspecific competition

As experiments with succession fields have shown, there is no tendency in 'Hybrid 207' to spread out into adjacent native vegetation. A comparable behaviour was observed in *T. koksaghyz* (Uhlemann et al. 2019). Over a period of six years (2015–2021), the *Taraxacum* flora around experimental fields at Julius Kühn Institute sites (Quedlinburg and Groß Lüsewitz, Germany) and *T. koksaghyz* breeding fields in Bavaria (Parkstetten, Sossau and Straubing) was continuously studied. Not a single plant of both *T. koksaghyz* and any *Taraxacum* hybrid was found within native *Taraxacum* populations. This result is confirmed by no reference of these taxa in the German floristic literature (Uhlemann 2021) despite the extensive cultivation of *T. koksaghyz* in the 1940s and 1950s.

In contrast, interspecific competition (competition with weeds) under experimental conditions in 'Hybrid 207' and *T. koksaghyz* is different. The inital number of 651 plants of *Taraxacum* 'Hybrid 207' decreased within the first year to 447 plants, presumably due to intraspecific competition. Finally, c. 350 plants survived, a decline of 46.2%, and formed a robust population. As already stated by Iaffaldano et al. (2018) the largely undomesticated *T. koksaghyz* competes poorly with weeds, which has been confirmed by Uhlemann et al. (2019). An initial number of about 1000 plants decreased within one year to zero after subsequent establishment of weeds.

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