Genetic resources in Finnish landrace rye (*Secale cereale*) and experimental evolving of its spring-habit from winter rye

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Rye was the most important grain crop in Finland towards the end of the 19th century. Rye was largely grown in burned lands, *kaski* (slash-and-burn) and *kytö,* in the past. In the primary form of *kytö*, shoveled topsoil was heated on fires slowly combusting extraneous wood, brushwood or reed, or in the secondary form, a dry upper layer of organic topsoil of field was burned in a prescribed frontal mode *in situ*. The *kytö* selected against the brittle spike type, largely eliminating the weedy seed banks in the soil. Likewise, seed handling, especially the common cleaning with a *pohdin* -device further eliminated partially brittle spike types and selected against weedy rye. Rye was a cash-crop for the peasants in the past and was mainly attempted to be exported as seed. The commonly used smoky *riihi*-drying sanitized and conserved grains, which retained germinabilty, and in part increased demand for seed abroad. The grains produced on burned lands were fortified with minerals, including the minor elements, and good winter-hardiness occurred in the Finnish rye. The immigrant Finns were probably the first since 1638 to grow rye from seeds brought along with them to New Sweden in North America, where de-domesticated or feral rye became a weed problem in the 1950s. Some genetically variable landraces could be sown during different times of the year, thanks to segregate plants adapted to different sowing-times. Sowing of a winter rye landrace in May, the season of spring grain sowing, enabled selection of spring-habit mutants or segregants, which could be used to establish a true-breeding spring stock of rye shown experimentally. In the past, mid-summer sowing could occur with co-cultivation, e.g. with the traditional slash-and-burn turnip as the first season crop, or the autumn seedling of rye could be used as pasture. The Finnish rye populations frequently had cytoplasmic male sterility (CMS) and nuclear restorer genes of anther fertility effective in the CMS. A non-leaky CMS and a leaky CMS (with male fertility in the late stems) are shown. Homozygosity obtained through forced self-pollination in a Finnish rye revealed unnoticed genes, such as dwarfs. A local rye population originating from Putkosjärvi area (64° 27’ N), in Ristijärvi Municipality, evidently devoid of the frequently contaminating weed, rye brome (*Bromus secalinus*), is thought to present an uncontaminated, ancient Finnish rye. The rye brome has contaminated growth in Finland at least since the Iron Age. Morphological variants, like brown spike or glume color and awnlessness were detected in the landrace. Two of 18 Finnish landraces were found to carry accessory or B chromosomes in a study in 1964. B chromosomes are known to interfere with the expression of some genes, perhaps also ensuring variation in the vernalisation needs of the plants.

Keywords: awnless rye, brown spike, cytoplasmic male sterility, de-domestication, glossy spike, hybrid rye, fertility restorer, monococcoid spike, *Secale segetale*, seed export, summer rye evolution

Introduction

Rye (*Secale cereale*) pollen appeared since 2170 ^{14}C years BC from the bottom sediments of Lake Ahmasjärvi, in Utajärvi Municipality (Reynaud & Hjelmroos 1980, 1981). This ^{14}C age corresponds to 3092–2278 cal BC at 94.6% probability when calibrated with the OxCal 4.3 (120) program. ^{14}C dated sediment tends to exaggerate the age, but in this age class was also shown to give too young ages from the sediments of a small lake studied in Finland (cf. Tolonen 1980). Other dated results of the prehistoric and early historic sites of rye in the territory of Finland were compiled, and the archaeological spreading routes of rye in and historically out of the country were described (Ahokas 2009). An old landrace studied in this paper originates from a farm lying 93 km of the Ahmasjärvi archaeological site. Charred grains involving a high proportion of rye were excavated in the center of the Turku (Åbo) town, a sample of which is in Fig. 1. Turku was a port and market town of Finland in the past. It encountered several fires as well as robbing by foreign military groups.

Because of the nearly obligatory cross-pollination, the evolving of the non-shattering rye form has required spatial isolation from the weedy, shattering forms, and drastic, long-lasting selection. Such requirements are not realized where shattering weedy or wild ryes are around. The ancient *kytö* fire culture and cleaning of seed with the *pohdin* -device and with other means may have played a crucial role in eliminating the weedy rye forms in Finland in the past (Ahokas 2012, 2018). Zhukovsky (1971) pointed out the difficulty of overcoming the shattering property of wild or weedy *Secale* species or forms: worldwide, there has been even 100 years of selection towards non-shattering rye in maintenance in botanic gardens without any notice of development of a non-shattering rye form.

In the ancient times, winter rye was sown in the spring at about the set of Dog's Constellation in Finland (Magnus 1555). The early sown winter rye, St. John's rye (*juhannusruis*) or midsummer rye was traditionally used as pasture or fodder in the first season sometimes grown as a mixture with other crops (Outhier 1746, Boije 1915, Grotenfelt 1922, Valle 1934, Charpentier 1941).

The immigrant Finns in New Sweden, present US Delaware and Pennsylvania, were probably the first to grow rye in America. In 1749, Peter (Pehr) Kalm interviewed old immigrants in America and recorded their memories (Kalm 1970). E.g. Peter Rambo the Elder was known to have brought rye among other seeds along with him to America in 1642. Since the family Rambo was later reasoned to originate from the Vaasa (Vasa) region in Finland, the rye may have been of the variety or brand 'Vaasa rye'. The Finnish Historian Zacharias Topelius (*1818 †1898) wrote about the high-quality 'Vaasa rye' ('Vasa råg') in a merchant's boat in Turku harbor in 1671 (Topelius 1899). Cneiff (1757, faximile in Ahokas 2009: p. 44–45) wrote about the export of 'Vaasa rye' ('Wasa-råg') with the synonym 'Österbottnisk råg' ('Ostrobothnian rye', 'Pohjanmaanruis') and another rye variety, 'Hållola-råg ifrån Nyland', i.e. 'Uudenmaanruis', 'Nylandsråg' and 'Hollola rye' varieties. The old Finnish rye sources were widely grown abroad around the Baltic Sea and spread further by the local traders (Ahokas 2009). E.g. in Russia in 1882 and in the Soviet Union in 1923 (Antropov and Antropov 1929, in Ahokas 2009: Table 10) the rye strains of Finnish origin were grown widely. These were 'Vaasa' ('*Ваза*'), 'Newland' ('Nylandsråg', 'Uudenmaanruis'), 'Ivanovskaya' (*Ivan* = '*Juhani*' in Finnish; the name refers to the Finnish *juhannusruis* sown on about St. John's day in June), and 'Kustovka', meaning 'tuft rye', in Finnish *ryväsruis*, *juureinen*, and other names, like *savokas* (Ahokas 2009). The many-stemmed *savokas* was sown sparsely ("with a shoe distance between seeds", S. Honkala in Virtaranta 1947). The Finnish 'Vaasa rye' was grown since the 18th century in Russia (Antropov and Antropov 1929: p. 291). In the statistics for 1815–1817, the export of rye and barley (*Hordeum vulgare*) grain was greatest via Vaasa port of the Bothnia coast in Finland (Frosterus 1819).

Trials with a number of Finnish landraces were arranged when the first foreign rye cultivars had been introduced to Finland. The best landraces were typically as productive as the foreign cultivars in local trials (Teräsvuori 1917, Simola 1922, Isotalo and Vogel 1962). In the trial field described by Teräsvuori (1917), also winter wheat (*Triticum* sp.) varieties were sown, but without results because wheat did not compete with weeds. The high and many-stemmed landrace rye is more competitive with weeds than wheat.

In 1980, 1981 and 1982, samples of old rye samples were collected in Finland for the Nordic Gene Bank. Many of them were not recognized to be known cultivars (Mikkola et al. 1991). Some previously ignored inherited characteristics of the Finnish landrace rye are described below.

Fig. 1. Charred grains, apparently mainly rye from archaeological excavations of the Medieval Turku (Åbo), a grain exporting town also subjected to robbing of grain in the history. Author's photo from the Aboa vetus exhibition, Turku. Sept. 30, 2009.

Results and discussion

Cytoplasmic male sterilities and the restorer genes of male fertility in Finnish landrace ryes

A number of cytoplasmic male sterilities (CMSs) in Finnish ryes were found in cv. ‘Ensi’ in 1976, when I actively looked for them in the field by feeling between fingers in the direction of the wider dimension of the spike; the sterile spikes feel soft, while male fertile spikes feel hard and plump. I isolated 27 putative CMSs (Fig. 2, Ahokas 1980). Cv. ‘Ensi’ was released in 1933, actually being a sample of the midsummer rye landrace grown by the farm of the Westermarck Manor in Järvenpää, Central Uusimaa Province, in 1918 (Pesola 1934). The word *ensi* (‘the first’) was written in field records as early as in 1919, because it emerged as the first, in four days’ time after the sowing (Anon. 1919–1920). Cv. ‘Ensi’ was ranked the best in the score of “useful protein %” among 20 ryes grown and studied in Poland (Kubiczek et al. 1975).

Figs. 2–5. Cytoplasmic male sterile (CMS) samples from Finnish ryes. – Fig. 2. CMS_{Ensi} isolate no. 24 (Ahokas 1980). Mature spikelets of a partially shattering or weedy *segetale* segregant of cv. ‘Ensi’ grown in the field in the 1977 season and harvested as spikes. This unrestored CMS_{Ensi} variant was open-pollinated in the original ‘Ensi’ population in the field in 1976. Rudimentary, collapsed anthers (dark in the photo) are usually retained with the grains to maturity in contrast to the fertile anthers which typically fall after the anthesis. Scale 2 × 20 mm. The insert shows a SEM view of a *segetale* spikelet of the *Triticum dicoccon* shattering type with the abscission tissues visible on segment ends of the rachis. Scale 0.5 mm. – Fig. 3. Male sterile (on the left) and restored spike of CMS_{Voima} from cv. Voima (Ahokas 1980). Grown in the greenhouse. June 1996. – Fig. 4. An unrestored $CMS_{Ristijärvi}$ spike from the landrace ‘Sulonruis’. The stamen filament usually does not elongate and the sterile anther remains in the flower. Grown in the field. June 26, 2011. – Fig. 5. Male fertile, restored (on the left), and male sterile primary spike, unrestored (center) and partially fertile, unrestored CMS spike of a late tiller (on the right), of the $CMS_{Finnråg}$ cytoplasm from the landrace ‘Finnråg’, NGB 2563. Grown in the field. July 15, 2011. The smallest squares are 1 × 1 mm in backgrounds in Figs. 4 and 5.

In 1977, I could isolate a further CMS from cv. ‘Voima’ (Fig. 3, Ahokas 1980), a cultivar bread in Finland. The Finnish rye landrace ‘Härmänruis’ (Walle 1930) might be the source of the cytoplasm.

Later, I isolated a CMS in the ‘Sulonruis’ landrace and its dominant restorer of fertility (Fig. 4). This $CMS_{Ristijärvi}$ is perfect in the tested environments, so that also the later tillers are male sterile. The original $CMS_{Ristijärvi}$ plant was open pollinated with ‘Sulonruis’. The next generation gave male fertile plants. These were sib-pollinated and resulted in 15 male fertile and 6 male sterile plants in the next generation. This segregation fits to a 3 : 1 ratio ($\chi^2_{(3:1)} = 0.143$, $p = .705$), suggesting that a dominant restorer gene of fertility was involved. In a further cross of $CMS_{Ristijärvi}$ × sib, heterozygous for the restorer, the F_1 segregation was 23 male sterile : 24 male fertile plants which fits to a monogenic backcross ($\chi^2_{(1:1)} = 0.021$, $p = .884$). I obtained but little seed from forced self-pollination of restorer-heterozygous plants with $CMS_{Ristijärvi}$ cytoplasm. Their S_1 plants segregated 7 male sterile : 9 male fertile plants. The ratio 7 : 9 fits to a 1 : 1 ratio according to the binomial test (one-tailed $p = .402$). A

$CMS_{Ristijärvi}$ male sterile was pollinated with the spring-habit derivative of ‘Sulonruis’ (see the later Chapter). The $CMS_{Ristijärvi}$ was effective also in the summer rye background.

I isolated a further CMS from the winter rye ‘Finnråg’ (NGB 2563), a sample of which was obtained from the Nordic collection of plant genetic resources, Alnarp, Sweden. The Swedish name ‘*Finnråg*’ means ‘Finnrye’. Numerous immigrating Finns brought seed material of crops especially in the 16th century to the Central Scandinavia (Ahokas 2009, 2012), or the original ‘Finnråg’ was exported from Finland. $CMS_{Finnråg}$ is leaky with the late tillers ultimately being male fertile, while the primary tillers are male sterile (Fig. 5). When I crossed the $CMS_{Finnråg}$ with the summer rye landrace ‘Vähä-Krekula’ as the pollen parent, the F_1’s were partially male sterile summer ryes. The 63 BC-F_1’s from four backcrosses with ‘Vähä-Krekula’ were all male fertile, suggesting that ‘Vähä-Krekula’ has a high frequency of restorer genes for $CMS_{Finnråg}$. The self-pollinated F_1 of $CMS_{Finnråg}$ /‘Vähä-Krekula’ segregated 4 summer and 2 winter plants, the summer types grown to maturity being male fertile, one of them being a dwarf; here, the pedigrees are marked according to Purdy et al. 1968. The F_1 of $CMS_{Finnråg}$/‘Vähä-Krekula’//‘Kerimäkeläinen’ produced 11 fertile and 4 male sterile plants, and another F_1, 14 male fertile plants. Thus, the summer rye ‘Kerimäkeläinen’ has both restorer and maintainer-of-sterility genes. F_1 male sterile plants of the cross $CMS_{Finnråg}$ /‘Vähä-Krekula’//‘Kerimäkeläinen’ were pollinated with fertile sibs resulting in the next generation, 87 male sterile, 9 leaky and 115 male fertile and 38 plants which were not classified, all plants of summer type. The segregation ratio of (87+9) : 115 fits to a monogenic backcross ($\chi^2_{(1:1)}$ = 1.710, p = .191). The emasculated leaky male sterile F_1 plants of $CMS_{Finnråg}$ /‘Vähä-Krekula’ pollinated with male fertile sibs resulted in 29 male sterile, 6 leaky, 27 male fertile, 21 unclassified summer and 17 unclassified winter plants. The segregation of (29+6) : 27 fits to a monogenic backcross ($\chi^2_{(1:1)}$ = 1.032, p = .310). Both ‘Vähä-Krekula’ and ‘Kerimäkeläinen’ evidently originate from eastern Finland.

B chromosomes in Finnish landrace ryes

Only one published study is known about the B, accessory or supernumerary chromosomes in Finnish landrace ryes (Iskari 1964). Comprising of altogether 900 studied cell divisions, Iskari showed two of 18 landraces to have plants with B chromosomes. If the occurrence of the B chromosomes is rare, they may also remain undetected in the smallest samples. Since also the Swedish variety named ‘Vasa II’ (Ljung 1930) having B chromosomes (Müntzing 1947, 1949) originated from the Finnish landrace rye ‘Vaasanruis’, in Swedish ‘Vasaråg’ or ‘Wasaråg’ (Ljung 1918, 1930), B chromosomes evidently existed in about 15% of the Finnish rye landraces. The frequency of B chromosomes in local ryes apparently increased eastwards from Europe (Kranz 1973). Various environmental factors, including plant density in the stand, are thought or shown to affect the number of B chromosomes in rye (Hutchinson 1975). The B chromosomes in rye are not neutral in their genetic effects, which have recently been confirmed (Carchilan et al. 2009, Ma et al. 2017).

Past strip field system and loan granaries ensured nearly panmictic pollination of rye in a village

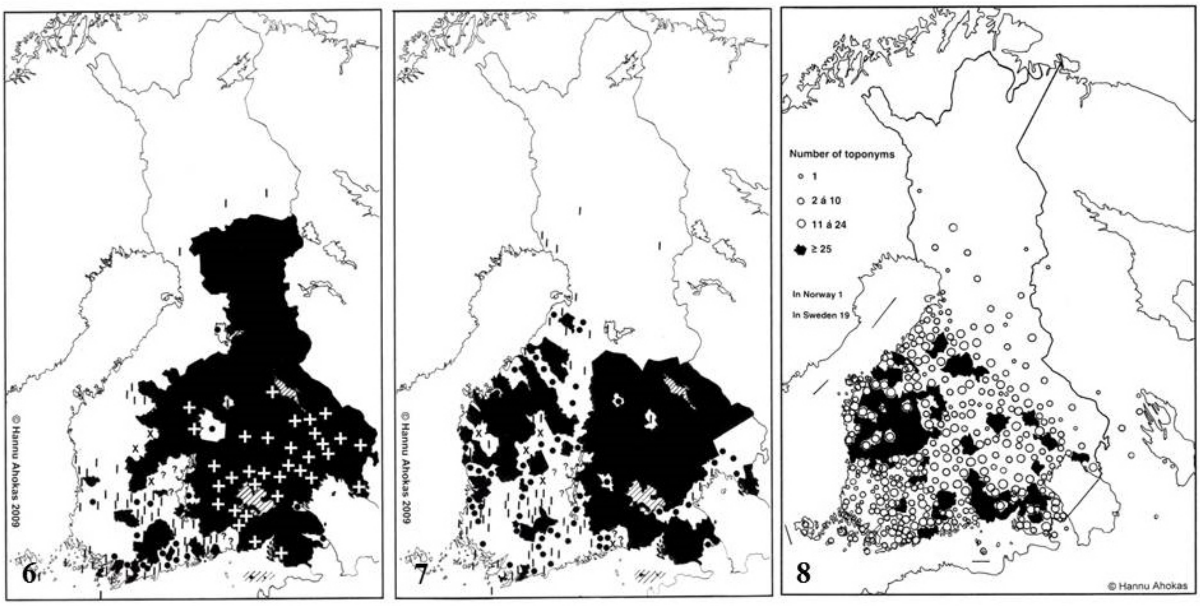
The widely used strip cultivation system of the peasants under their landlords led to the crop growing of different houses side by side making cross-pollination of different seed stocks of rye unavoidable (Ahokas 2001, 2009). The loan granaries were used since the early 18th century operating sometimes until the 1950s. In the loan granary of a village or a municipality, different grain lots of a crop species were mixed together, and with the older stocks. When such grains were used as seed, they were already a genetic mixture.

Cultivation on fire lands and seed cleaning selected against shattering or *segetale* spike type and weeds

De-domestication or evolving of shattering grain crops sometimes associated with increased seed dormancy has occurred especially in monoculture management in cultivated rice species (*Oryza* spp.) and rye (Ahokas 2018). The wide growing of rye in *kaski* (slash-and-burn) and *kytö* fire lands (Figs. 6–8) along with seed cleaning in Finland in the past selected against the shattering weedy or *segetale* type of rye and weeds in general. Tendency to form weedy swarms has remained in the cultural rye. A case of de-domestication in rye was described in Kazakhstan (Shipchinsky 1929). Weedy or feral rye became a problem in USA especially in wheat fields with a monoculture character since the 1950s.

In the primal form of *kytö* burning, the topsoil is slowly heated on flameless fires, and later, on organic soil types, the dry top layer was burned with a frontally proceeding manner (Ahokas 2010, 2012). The *kytö* largely destroyed weeds and their seeds. The *pohdin* -device for cleaning of grains was commonly used in Finland in the past among other methods. The *pohdin* was illustrated in my representation (Ahokas 2018). The competition by the high-stemmed rye declined weeds in the rye canopies.

It may be noted that the distribution of the prehistoric rock paintings known by 2012 correlates (Spearman rank order correlation) highly significantly with the local percentage of rye growing in *kaski* and *kytö* fields in 1833–1834, with a somewhat less strong correlation with the *kytö* percentage (Ahokas 2012: Table 6). This indicates a prehistoric origin of the fire land cultivation.



Figs. 6–8. Traced fire cultivation areas in Finland in the boundaries of the era. – Fig. 6. The *kaski* (slash-and-burn) area of rye in different municipalities in 1833–1834 according to the manuscripts of Böcker (ca. 1835) compiled by me: I = 0.1–4.9%; • = 5–9.9%; ▌ = 10–70%; x = proportion unknown; ? = data of the municipality unavailable. The municipalities where the proportion on *kaski* and *kytö* (see Fig. 7) area together was 60% or more of rye are indicated with white crosses. – Fig. 7. The area of rye in *kytö* -burned fields in different municipalities in 1833–1834 according to the manuscripts of Böcker (ca. 1835) compiled by me: I = 0.1–4.9%; • = 5–9.9%; ▌ = 10–50%; x = proportion unknown; ? = data of the municipality unavailable. – Fig. 8. A map showing the distribution of 8058 toponyms based on *kytö* in traditional parishes within the 1920 Tartu Peace boundaries. The marks are given on the map with their limits: 1, 2–10, 11–24 and ≥25 toponyms. The *kytö* burning is a prehistoric method in Finland. Only few additional *kytö* -toponyms occurred in Sweden, Norway and Soviet Union, which also suggests the *kytö* burning to be a Finnish practice. Earlier published in Ahokas 2009, 2010, 2012.

The past cultivation on fire lands and drying of harvested crop in heated, smoky *riihi* controlled ergots and fusaria, conserved grains and seed germinability

The fire land ensured mineral nutrition, in studied *kaski* soil for three, up to five years. *Kaski* and *kytö* burning practically destroyed sclerotia of the ergot fungus (*Claviceps purpurea*) in the soil. The soil availability of microelements also increased in fire cultivation. The microelements are carried at the minimum required level over about three successive generations if used as seed in field growing. A good availability of boron enhances anther and pollen fertility, which in turn decreased the occurrence of the poisonous ergots. In the beginning, the smoky heat of a Finnish *riihi* (a crop drying house with a hearth) reached 55–60 °C, and later higher temperature during the heating lasting usually one night or day (Grotenfelt 1899). Another article gives 60 °C as a typical *riihi* temperature (Löthner 1889). Material generating intensively smoke was often burned in the hearth for lots used as seed of the crop. Fungal diseases, including ergots and fusaria (*Fusarium* spp.) were principally rendered to lethality. Invertebrates in the crops died and mostly fell from the sheaves on the floor during the heating in the *riihi* house.

Excellent winterhardiness detected in Finnish rye landraces

The root properties were studied in two highly winterhardy Finnish landraces, 'Iisalmiroggen' ('Iisalmenruis') and 'Otsolaroggen' ('Otsolanruis'), and two cultivars locally moderately or poorly winterhardy, German 'Petkuser' and 'Veredelte Vasaroggen', bred in Svalöf (Kokkonen 1927), a mild-winter region in South Sweden from the 'Vaasanruis' introduction. Kokkonen found that good winterhardiness is associated with extensible roots. The Finnish landraces were the most tolerant in the freezing experiments on winter rye seedlings done in Sweden (Åkerman et al. 1935).

Forced self-pollination recalls odd types from rye landraces

The self-fertility in Finnish ryes is low. Inbreeding of rye leads to homozygosity of genes, e.g. dwarfing genes, otherwise remaining unnoticed in the population. Inbreeding of rye was necessary to make the productive modern hybrid rye cultivars, which also require CMS, its restorer gene of male fertility and may also need enhancers of pollen shower to avoid partial grain set and subjecting to infest with ergot conidia.

An ancient, variable rye from Ristijärvi Municipality, beyond 64° N latitude

I purchased a sample of the rye 'Sulonruis' having its weed seeds from the last farmer maintaining it. According to him, the rye originates from Putkosjärvi area (64° 27' N) in Ristijärvi Municipality, and it has evidently been grown on a single farm since the end of the 19th century. Putkosjärvi is 93 km ESE of the Ahmasjärvi site with evidence for a prehistoric rye (see Introduction), and 74 km ESE of Nimisjärvi, another site with prehistoric rye growing (Reynaud & Hjelmroos 1980, 1981). 'Sulonruis' rye sample was devoid of rye brome (*Bromus secalinus*), a weed frequently contaminating rye in the past, and also therefore 'Sulonruis' represented an uncontaminated, ancient Finnish rye.

Figs. 9–13. Spike and grain variants in 'Sulonruis' landrace. – Fig. 9. The rare purple anther color of the dimorphism having mostly yellow anthers shown in the insert. June 22, 2010. – Fig. 10. Monococcoid spike on the right with incipient yellow maturity, while the typical dicoccoid spike was still green on the left. July 3, 2011. – Fig. 11. Variation in epicuticular waxiness on spikes. Highly waxy and anthocyanin rich on the left, and glossy spike marked. July 2, 2011. – Fig. 12. Occurrence of red anthocyanins in immature grains. July 2, 2011. – Fig. 13. Mature spike color, from straw-light to dark brown, and awn variants. In the center, an anwless spike. Scale 5 × 25 mm. The inserted SEM view shows the awnless lemma tip. Scale 0.5 mm.

Seeds of rye brome occurred commonly especially in the *juhannusruis* rye in the 20th century (Grotenfelt 1916) sometimes exceeding the rye seed proportion, the rye brome being on its way to become a grain crop (Ahokas 2009: p. 10). The rye brome, now an endangered species, developed to a weed species in Europe (Koch et al. 2016). It infested arable land in Finland at least already in the 887–1014 AD (Vanhanen 2010). Exported Finnish rye seed may have spread this weed in the past. Morphological variation was wide in the landrace (Figs. 9–13). Variants in anther color (Fig. 9), epicuticular waxiness including glossy (Fig. 11), spike types and densities, brown spike (glume), awn length and awnlessness, were detected (Fig. 13). Monococcoid spike types occurred and appeared to mature earlier than the typical dicoccoid plants (Fig.10). The grains showed purple anthocyanin color in part of the immature spikes (Fig. 12). Brown spikes appear in ‘Sulonruis’ (Fig. 13) and were also observed by Linkola (1919–1920) in Finnish ryes.

Notably, Vavilov (1926) and Antropov and Antropov (1929) did not know brown spike color or glossy (“without waxy bloom”) types in the variation of the European rye, or an awnless rye worldwide.

A CMS cytoplasm and the dominant restorer gene of anther fertility occurred in ‘Sulonruis’ (see the separate Chapter). Segregation of summer rye from ‘Sulonruis’ is presented in the next Chapter.

Spring-habit segregants from ‘Sulonruis’ to breed a summer rye

The early sowing in the spring may have been the way to attain a spring-habit rye by the early growers in Finland. Here I show the possible way of breeding such spring rye from ‘Sulonruis’ (Figs. 14–17, Table 1). The three crossed primary parents (Fig. 14) produced 26 winter-habit and 76 spring-habit plants which fits to a 1 : 3 ratio ($\chi^2_{(1:3)} = 0.013$, $p > .90$). Thus, the spring-habit gene is dominant. The parents were all heterozygous for the chlorotic gene and therefore their spring-habit gene evidently came from a single lineage. Some of the chlorotic segregants died after the seedling stage (Table 1).

Figs. 14–17. Selection of spring habit from ‘Sulonruis’ winter rye. – Fig. 14. From the rye sown on May 8, 2011, three plants bolted by June 25 (marked with arrows). – Fig. 15. These three plants were crossed in pairs and the seeds grown under growth lamps at room window, where the temperature did not sink under +18 °C avoiding chill vernalization. All the crossed pairs segregated a fine-stripe, chlorotic leaf mutant (marked with rings) at the seedling stage suggesting that the three seed-parents originated from a single lineage. March 27, 2012. – Fig. 16. The plants segregated winter-habit and spring-habit plants in a ratio of 1 : 3, the latter being freely pollinated by sibs. May 29, 2012. – Fig. 17. The seeds from 2012 were sown in the field, the Medvastö Farm, Kirkkonummi on May 14, 2013. As expected, they still segregated a minority of chlorotic seedlings, and of winter types appearing as rosettes at the base in the grain-filling stage of the spring-habits segregants on July 18, 2013.

Table 1. Segregation of winter vs. spring habit and chlorotic seedlings in F_1 generation of the three crossed plants bolted from the spring sown winter rye. The F_1 was grown under non-vernalizing environment without temperature decline under +18 °C (Figs. 15 and 16). Four of the chlorotic seed-lings died.

Crossed plants (no.)	Chlorotic : green at seedling stage	Winter : spring habit at 4 months' age
1 × 2	9 : 40	18 : 31
2 × 1	9 : 25	4 : 26
3 × 2	3 : 2	0 : 5
2 × 3	2 : 16	4 : 14
Total	23 : 83	26 : 76

A strain from Ilomantsi Municipality, North Karelia Province, Finland, was obtained in 1980 as a summer rye, but proved to be mainly winter rye when grown in the more southern and more maritime environment in Viikki, Helsinki (Mikkola et al. 1991). This may have represented an ancient Finnish rye type segregating both summer and winter types and permitting sowing in the spring and harvesting both in the first, and after hibernation, in the second season. Sometimes patches destroyed by adverse winter conditions in a field of winter rye were sown in the spring with summer rye in (Grotenfelt 1922), which may have led to mixtures of winter- and spring-habit and segregation. A spring-habit offtype was also found from the *juhannusruis* (St. John's rye) winter rye sample from the Lohja Municipality sown on July 21, 1919 (Linkola 1919-1920). In winter rye sown in spring or summer, heading was frequently observed in the sowing season by peasants. A special Finnish name *maakalainen* was recorded for such a deviating segregant (S. Honkala in Virtaranta 1947).

Ancient Finnish rye tolerated a wide range of sowing times, being sown principally in June in the ancient times (Magnus 1555), the sowing in June declining to 4.8% by 1950 (Ahokas 2009: Table 5). 'Sulonruis' was shown to adapt to a wide range of sowing times of the year in southern Finland requiring only some unfrozen topsoil (Ahokas 2011). The best results were obtained from late sowing, from mid-September to mid-November in Jokioinen, SW Finland in two year trials. Attacks of seedlings by insects, especially by *Oscinella frit*, and by diseases may make sowing of winter rye adverse in some periods of the summer.

Spring-habit or summer-annual rye was a minor crop grown especially in *kaski* (slash-and-burn) soils in Finland in the 19th century (Grotenfelt 1922). The high-yielding summer ryes grown in 1888–1915 by the Finnic Ingrians, Votians and Finns beyond the south-eastern boundary of Finland against Russia were probably mostly of old Finnish origin (cf. map 8 in Antropov and Antropov 1929).

Introducing of landraces and old varieties back to growing and to grain culture

There have been activities to find the last landraces by some researchers and members of the Maatiainen ry society in Finland and to spread the survived strains to cultivation. Likewise, e.g. in France (Bonjean 2018) and in the Nordic countries (Tvengsberg 2010) activities have revived rye landraces and old varieties. The 'Tvengsberg' rye has evidently a Finnish *kaski* rye origin being brought by immigrating Finns to Norway. However, the EU legislation protects plant-breeding companies and restricts wide trade of landrace seed.

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