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Onset of growth of bulbils in the field garlic (*Allium oleraceum* L.)

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The field garlic, *Allium oleraceum* L. (Amaryllidaceae), is a bulbous geophyte with a widespread distribution in Europe. The species mainly reproduces vegetatively by the formation of bulbils. Two cytotypes (tetraploids and pentaploids) with differing distributional patterns occur in Finland. A clear morphological difference between the two cytotypes can be seen in Finland, but in Central European populations no such difference has been reported. This study examined the onset of growth in bulbils and possible differences between the cytotypes. Bulbils for the experiment were collected from a mixed population with both tetra- and pentaploid plants and from a tetraploid population that has been observed to differ morphologically from other tetraploid Finnish populations. The results show that there is a difference between the timing of the onset of growth between the examined populations. The exhibited differences between the populations may indicate that the cytotypes are adapted to different winter climates. The atypical tetraploid population clearly differed from the mixed population and may thus be of a different origin than other Finnish populations. The atypical population could have been introduced with ballast. Further studies of plants of Nordic and Central European origin are needed to draw conclusions about the Nordic cytotypes.

The field garlic, *Allium oleraceum* L., is a bulbous geophyte with a widespread distribution in Europe. In the Nordics the species is fairly common in the nemoral and boreonemoral zones – in Norway there have been scattered observations up to latitude 70° N, in Sweden there are observations up to the latitude of 64° N (Umeå) and in Finland up to the latitude of 63° N (Vasa/Vaasa) (Hultén 1971, Mossberg & Stenberg 2018). The field garlic occurs on a rather wide range of different habitats, with a preference for habitats influenced by the activity of man. The species grows in dry and mesic meadows, in pastures, on cliffs and rock meadows, on roadsides and in some types of deciduous forests. The species favours, but is not exclusively bound to, calcareous substrates. (Hæggström & Åström 2005, Åström et al. 2015, Mossberg & Stenberg 2018).

The field garlic exhibits several levels of polyploidy, ranging from triploids to octoploids (2n = 24, 32, 40, 48, 56 and 64); of the reported cytotypes tetra-, penta- and hexaploids are the most common (Duchoslav et al. 2013). In the Nordics only tetra- and pentaploids have been reported (Åström et al. 2015). Both cytotypes are common in Finland. In Sweden 18 of the 19 investigated populations were pentaploid, in Norway both cytotypes has been observed and in Iceland the two investigated populations were tetraploid (Laane & Lie 1985, Åström et al. 2015).

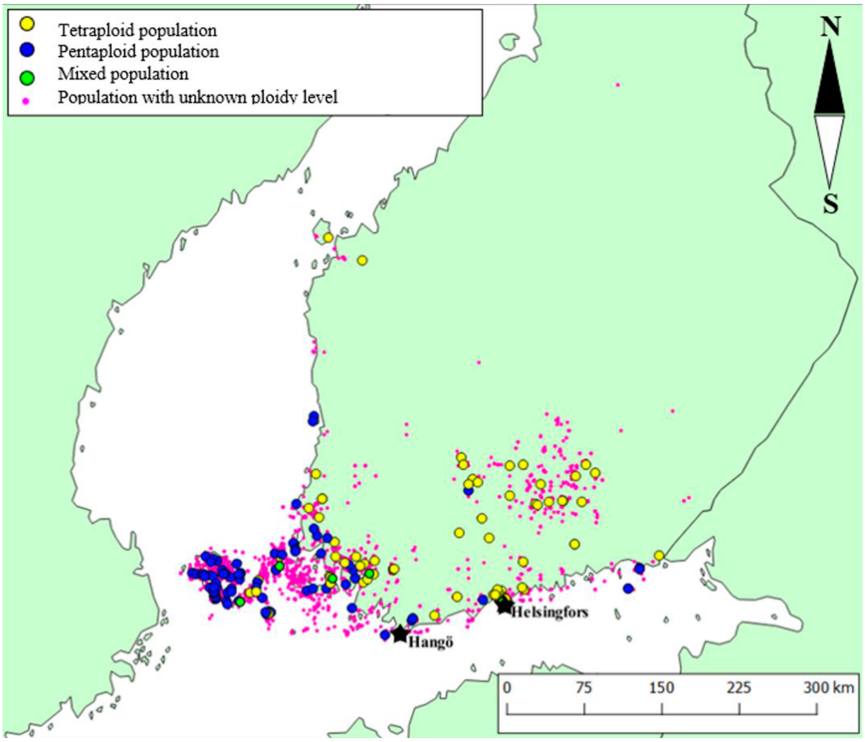

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Fig. 1 The distribution of field garlic and the two cytotypes in Finland, according to Åström et al. 2015. The sites of collection the bulbils for the experiment, Sveaborg in Helsingfors and Tvärminne at Hangö marked with black stars.

Rather comprehensive studies on the ploidy levels of populations of the field garlic have been made in Finland, and there is an evident difference regarding the distribution between the two cytotypes (Fig. 1). Most populations only consist of one of the cytotypes, but there are also mixed populations. Pentaploid populations are mainly bound to the Åland Islands and the S and SW archipelagos and coastal areas of the Finnish mainland. Tetraploid populations are more mainland bound with occurrences in the inland and along parts of the Finnish coast. Of the investigated Finnish populations 43,7 % consists of tetraploids, 51,6 % of pentaploids – only 4,7 % are mixed populations consisting of both cytotypes (Åström et al. 2015). Based on these findings and those from neighbouring countries, it has been suggested that pentaploids were introduced to Finland from the west, from Sweden via the Åland Islands to the Finnish mainland along the coast of Nyland (Uusimaa). Accordingly, the tetraploid populations in Tavastland (Häme) are tied to locations connected to Iron Age activity and historical trade routes and could thus be of eastern origin. The species is hence an archaeophyte in Finland (Åström et al. 2015).

Differences in morphology and ecology between the cytotypes have been studied to some extent. No morphological differences between cytotypes have been observed in Central Europe; however, signs of some ecological differences have been reported (Duchoslav 2001a, Duchoslav 2001b, Karpavičienė 2002, Duchoslav 2009, Duchoslav et al. 2010, Šafářová et al. 2011, Duchoslav et al. 2013, Fialová & Duchoslav 2014, Duchoslav & Staňková 2015, Ježilová et al. 2015). In Finland and the Baltics, a distinct morphological difference between tetraploids and pentaploids has been observed (Fig. 2 a–b). The tetraploid cytotype is on average relatively low in height and produces usually numerous small greenish bulbils and few white flowers whilst the pentaploid cytotype is, on average, taller and produces fewer but larger reddish purple bulbils and many pink to violet flowers (Åström & Hæggström 2004, Hæggström & Hæggström 2010, Karpavičienė 2012). There is also a difference in regard of seed production between the cytotypes (Hæggström & Hæggström 2010). Differences regarding ecology in Finnish conditions has only been studied to a limited extent. On Sveaborg (Suomenlinna) in Helsingfors (Helsinki)

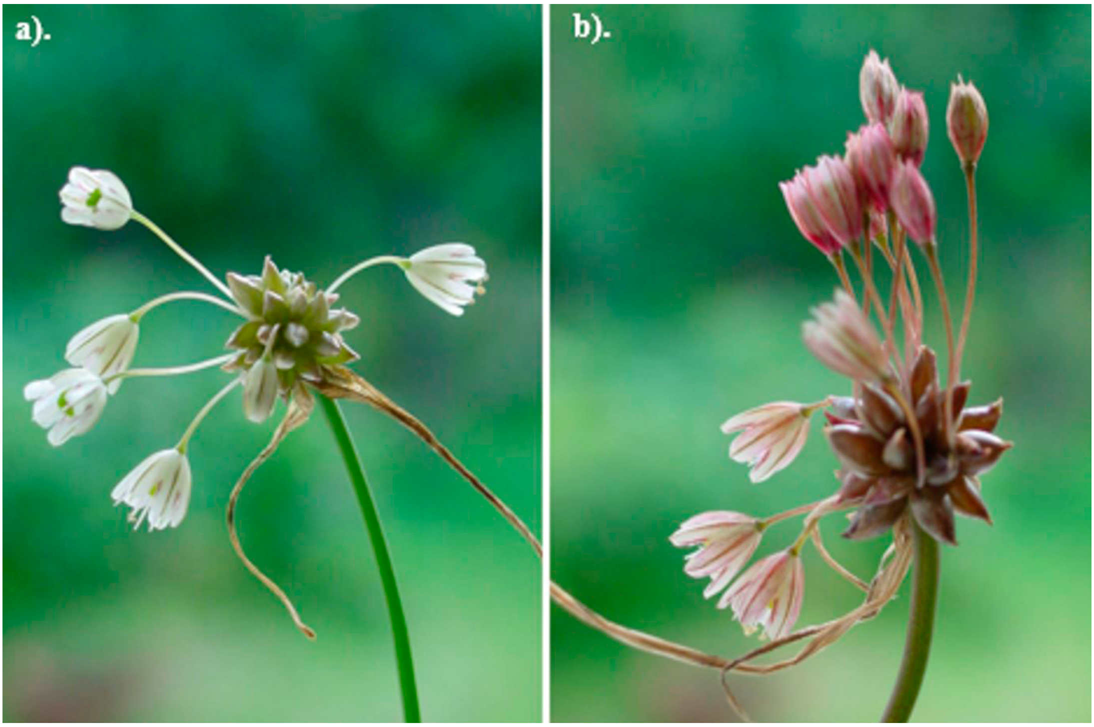


Fig. 2a–b. Field garlic in bloom of the a) tetraploid and b) pentaploid cytotype. The two cytotypes differ in Nordic conditions; tetraploids have fewer, almost white flowers and usually numerous, small, greenish bulbils, while pentaploids form more and pink/violet flowers and fewer and larger reddish purple bulbils. Photos: Carl-Adam Hæggström (20/8/2001, Finland, Åboland, Nystad, Varhela, meadow at Eskola).

there is a tetraploid population that has been observed to differ both in ecology and morphology from other tetraploid populations studied in Finland (Åström & Saarinen manuscript)

The annual cycle of the field garlic

The field garlic reproduces both vegetatively and generatively. The vegetative reproduction takes place through the formation of bulbils in the inflorescence and though the formation of subterraneous daughter bulbs. The formation of bulbils is the most significant way of reproduction in the species (Åström & Hæggström 2004, Fialová & Duchoslav 2014). The field garlic only produces seeds to a lesser extent and this is strongly correlated with the presence of pollinators. In the event of severe drought, the species only reproduces vegetatively (Åström & Hæggström 2004, Fialová & Duchoslav 2014). Despite the published evidence of the seed setting in the species, the misconception of the field garlic being seed sterile is still being published (Mossberg & Stenberg 2018).

After blooming and possible seed set, the above ground plant withers. Further growth starts from an axillary bud in the bulb and from the numerous bulbils formed in the inflorescence. The bulb can also form daughter bulbs that are eventually detached from the mother bulb. The growth is initiated by the formation of contractile adventitious roots that pull the bulbils and daughter bulbs into the ground. If the weather conditions are favourable, further vegetative growth onset starts during the autumn and leaves can then form and will thus overwinter under the snow. If there has been no above ground growth during the autumn, the daughter bulbs and bulbils simply overwinter below ground. Further development takes place in spring by the formation of up to five leaves. The plant is then capable of assimilation and stores energy in the subterraneous bulb. During the second summer, the plant is capable of producing an inflorescence with both bulbils and flowers (unpublished results). The flowering mainly takes place after the leaves have wilted – which in Finland takes place by the end of July or early August (Åström & Hæggström 2004, Alho 2009, Åström et al. 2012).

If the field garlic produces leaves in the autumn, these overwinter under the snow as wintergreen leaves and are also capable of growth during mild spells in the winter (Alho 2009, Åström et al. 2012). The snow cover is an efficient isolator and therefore a rather significant difference in temperature between the air and the environment under the snow cover can be observed – in addition, part of the light penetrates through the snow cover which enables assimilation (Starr & Oberbauer 2003, Saarinen et al. 2016). The capability of assimilation during winter or a quick onset of growth during times of favourable environmental conditions are clear competitive advantages.

The purpose of this study was to examine possible differences in regard of bulbil mass and timing of the onset of growth between tetra- and pentaploids from a mixed population and further differences to an atypical tetraploid population.

Material and methods

Collecting bulbils

The bulbils used in this experiment were collected from populations with known chromosome numbers (Åström et al. 2015). Bulbils from tetra- and pentaploid individuals were collected from a mixed cytotype population at Tvärminne, Hangö (Hanko) in the southwestern part of Finland. The two cytotypes were identified by differences in their morphology (Åström et al. 2015). The bulbils were collected from a mixed population to eliminate differences in local microclimates as a factor in the experiment.

In addition, bulbils were collected from a morphologically atypical tetraploid population on Sveaborg (Suomenlinna) in Helsingfors (Helsinki). There have been indications that the atypical tetraploid population on Sveaborg also differs in regard of certain ecological aspects (Åström & Saarinen manuscript).

The three cytotypes of this experiment will from now on be referred to as Tv-32 (tetraploids from Tvärminne, Hangö), Tv-40 (pentaploids from Tvärminne, Hangö) and Sv-32 (atypical tetraploids from Sveaborg, Helsingfors).

Weighing and planting of bulbils

At the start of the experiment, 80 randomly chosen bulbils of each cytotype were separately weighed with 0.1 gram accuracy. The growth experiment was started shortly after the weighing by planting the bulbils. The bulbils were planted at a depth of 5 mm in planting trays with individual wells with drainage. Commercial potting soil was used as a planting substrate. The trays were placed outdoors within an enclosure in Vik (Viikki) in Helsingfors. The plants were watered when needed.

The growth experiment was started in mid-September. Bulbils of Sv-32 were planted on 14/9/2018 while the bulbils of Tv-32 and Tv-40 were planted on 17/9/2018. In all, 648 randomly chosen bulbils of each cytotype were planted – of these 108 were kept outdoors during the entire experiment while the rest were used for other experiments (Sjöblom 2020).

Follow-up of the onset of growth from autumn to spring

After planting the bulbils, the trays were regularly controlled for any signs of onset of growth. In this experiment, onset of growth is defined as the timepoint at which the first leaf has been formed and is visible above soil. Controls for onset of growth were done from mid-September to the end of April. During the autumn, controls were done with intervals of 1–4 days depending on the rate of bulbils that started growing at the period. The last control of the autumn was done 11/12/2018 – the permanent snow cover that formed just after that made further controls impossible. In the spring controls were similarly done with an interval of 5–8 days, starting 4/4/2019 after the snow covered had melted and carried on until 25/4/2019.

Temperature data and snow cover

The temperature data was collected at the site of the experiment in Vik in direct connection to the field garlics during the entire duration of the experiment. The above-ground temperature at an elevation of 10 cm was tracked during the duration of the experiment. Only the above ground-temperature was tracked as this is the actual temperature that the plants are subject to. The temperature was tracked using two separate temperature sensors (iButtons®, DS1922L-F5 thermochrons; Homechip Ltd., UK) protected by a radiation cover made of a white PVC tube (length: 20 cm, Ø: 6 cm). The temperature sensors were placed one on either side of the experiment area. The temperature was recorded hourly.

Data on snow cover and depth in Gumtäkt (Kumpula) in Helsingfors (approx. 4 km SW of the experiment site) were downloaded from the open database of the Finnish Meteorological institute.

Statistical analyses

The results were statistically analysed using ANOVA and Tukey hsd (weight of bulbils) and survival analysis and Mantel-Cox (onset of growth) with the software IBM SPSS Statistics 25.0.

Temperature and snow depth during the experiment

During the beginning of the autumn, during the first two weeks of the experiment, the mean temperature was above 10 °C (Fig. 3). During the same period, the maximum temperature rose above 20 °C most of the days and the nocturnal temperature rarely fell below 5 °C.

As the autumn proceeded the temperature gradually sank, the first night with a sub-zero temperature took place 29/9/2018, after which some further nights with freezing temperatures occurred during the following weeks, but the daily mean temperature stayed at 5–10 °C. The weather stayed rather mild until the end of November, after which the mean temperature mainly stayed below 0 °C.

The first half of December was likewise rather mild in regard of the mean temperature, which stayed over 0 °C during many days. The first snow fell 13/12/2018. The snow cover was rather thin until the end of the year, when the depth of the snow increased to more than 20 cm. As the snow cover became thicker during the first half of January, the snow cover functioned as an insu-

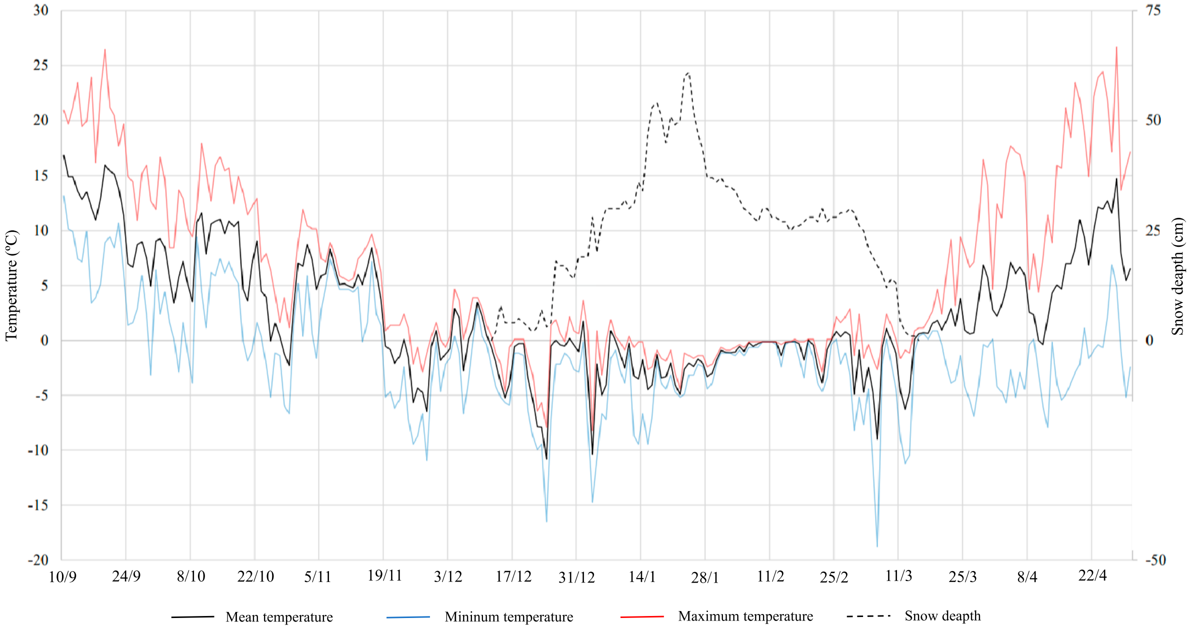


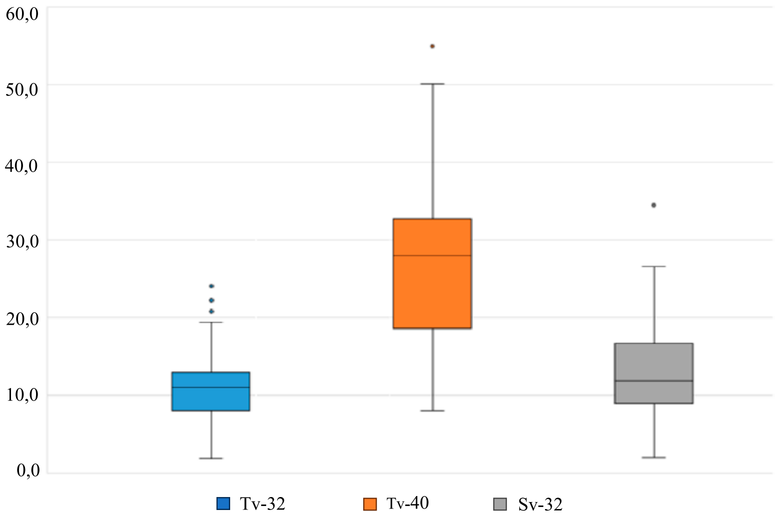
Fig. 3. The mean (black line), maximum (red line) and minimum (blue line) temperatures and snow depth (dotted black line) at the experimental site in Vik, Helsingfors during the duration of the experiment from September 2018 through April 2019.

lator, which means that there were not any large fluctuations in the temperature at ground level before the beginning of March. There was a permanent snow cover from the first snow fall in December until the snow melted in the middle of March. During the first half of January, the thickness of the snow cover exceeded 25 cm, whilst the snow cover grew to a thickness over 60 cm during the second half of the month. Throughout February, the depth of the snow cover exceeded 25 cm. While the snow cover was thick the temperature was stable and mainly fluctuated between 0 °C and –5 °C, with occasional drops down to –10 °C. The snow cover started melting at the end of February and had completely melted by mid-March. As the snow cover had melted, strong fluctuations in temperatures were again observed. The days became warm, but the nights were often still cold with many observed nights with sub-zero temperatures. The mean temperature was nevertheless always above 0 °C after the melting of the snow cover, and the observed maximum temperature was usually above 15 °C.

Morphological differences between the cytotypes

Clear differences between the three cytotypes in regard of the weights of the bulbils were observed (Fig. 4). The bulbils of Tv-40 clearly had a greater mass than the bulbils of Tv-32 (p <0,001) and Sv-32 (p <0,001), even though the observed variation was large. The bulbils of Sv-32 tended to have a smaller mass than the ones of Tv-32, but this difference was not significant (p = 0,246).

In addition, there was also a difference in colour of bulbils between the cytotypes of the mixed population (Fig. 5).



◀ Fig. 4. The fresh weight of the bulbils of the three different cytotypes of field garlic in the experiment. The analysis of the weight was done by weighing 80 randomly chosen bulbils of each cytotype.

▼ Fig. 5 Randomly chosen bulbils of each cytotype to illustrate differences in colour/hue. Scale 1 cm. Photo: Robin Sjöblom, 17/9/2018.

Onset of growth from autumn to spring

Onset of growth was observed for all three cytotypes in the autumn, but the time of the onset of growth and the share of bulbils for each cytotype that started growing differed clearly between the cytotypes (p <0,001, Fig. 6). Onset of growth was first observed for Sv-32 already 14 days after planting. After the first observation of the onset of growth, further bulbils were observed starting to grow at a high rate. More than 92 % of the bulbils of Sv-32 had started growing within 24 days after the onset of growth had begun. For the other two cytotypes, only a small share of the bulbils had started growing at this point. At the last observation point just before the formation of a permanent snow cover, the onset of growth had been observed for 97.8 % of the bulbils of Sv-32.

The very first observation of growth for Tv-32 occurred 25 days after planting the bulbils and for Tv-40 35 days after planting of the bulbils. Thus, the first observation of onset of growth took place clearly later than for the two cytotypes from Tvärminne than for Sv-32. The share of the onset of growth during the autumn grew steadily for Tv-32 and Tv-40. The pace at which new bulbils started growing was nevertheless clearly slower for these cytotypes than for Sv-32. At the last observation, 46.6 % of the bulbils of Tv-32 had started growing and the corresponding number for Tv-40 was 35.6 %.

In the spring, no further onset of growth was observed for Sv-32, because the large majority of the bulbils of this cytotype had already started growing in the autumn (Fig. 6). For Tv-32 and Tv-40, onset of growth was observed in the spring with a similar rate for the two cytotypes. At the last observation, 89.8 % of the bulbils of Tv-32 had started their growth and for Tv-40 the corresponding share of bulbils was 75.0 %.

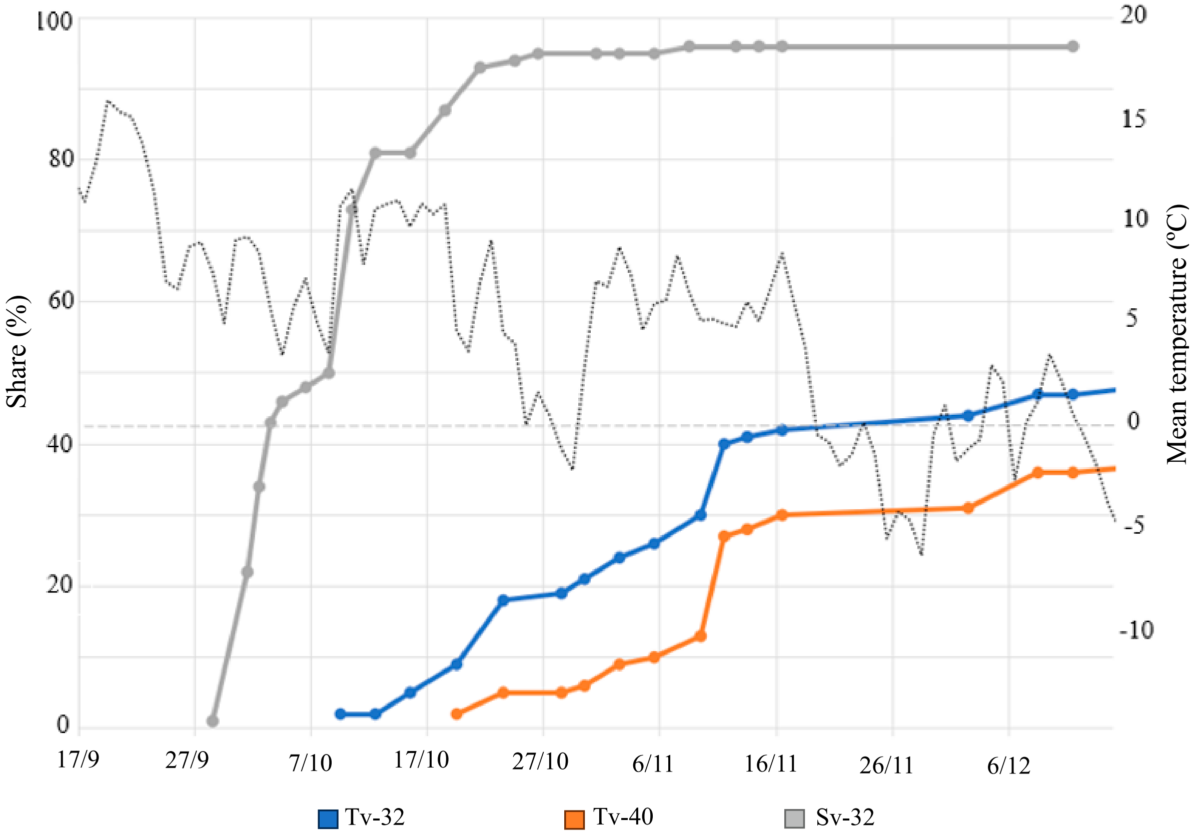


Fig. 6. The share of bulbils of the three cytotypes for which onset of growth was observed for over the cause of autumn 2018. The mean temperature is marked with a dotted line.

Differences between teraploids and pentaploids

The bulbils of the three cytotypes could clearly be distinguished from each other using their morphological traits, in line with earlier published findings (Åström & Hæggström 2004, Hæggström & Hæggström 2010). With rising ploidy levels, an expansion in cell volume is usually seen (Levin 2002), which could be the explaining factor of the observed differences in fresh weight between the cytotypes in this study. In the Baltics, corresponding differences between the cytotypes have also been observed (Karpavičienė 2012), while no such difference has been observed in Central Europe (Fialová & Duchoslav 2014), which would mean that the difference in ploidy level is not the only explaining factor for the observed differences in this study.

The measured weight of the bulbils was clearly lower than observations from previous years (Åström & Saarinen manuscript). The exceptionally hot and dry summer (Finnish Meteorological institute 2020) that prevailed before the collecting of the bulbils is probably one of the most contributing factors to this observed difference. The most noticeable difference was observed for Sv-32. This tetraploid cytotype has clearly differed during earlier years from other tetraploids, but in this study a significant difference in mass was not observed. An explanation for the lack of difference may be that the habitat in which Sv-32 grows is a rock meadow, which is heavily affected by drought, whilst the habitat of Tv-32 is of mesic character, which is not affected by drought to the same extent.

The observed differences in regard of the timing of the onset of growth between the three cytotypes may be explained, at least partly, by the fact that the different cytotypes are adapted to their main distribution areas. Pentaploid populations of field garlic in Finland mainly occurs in the archipelago with a coastal climate, while tetraploid populations occur to a further extent to the inland with a more continental climate, where winters are harsher and with a more continuous snow cover (Kersalo & Pirinen 2009, Åström et al. 2015). The presumed adaptation may have arisen through selection after the event of dispersion, as the cytotypes would then have been subject to different weather conditions. The differences in distribution may also be a result of significant changes in ecological niches between the cytotypes as they formed. Sudden changes in ecological niches are often seen when changes in ploidy levels occurs (Soltis et al. 2003, Ramsey 2011).

An early onset of growth is of great importance in the competition with other plants in the spring (Körner et al. 2008) as a late onset of growth might lead to being shadowed by other plants which would negatively affect assimilation. If the growth starts in the autumn, assimilation and growth can then quickly be resumed when the circumstances are again favourable in the spring (Saarinen et al. 2011). If the plant is subject to harsh winter conditions, for example to cold, onset of growth in the autumn might be a disadvantage as the plant may get damaged (Burke et al. 1976; Sakai & Larcher 1987). A permanent snow cover protects the plants from severe cold due to the insulating effect of the snow cover (Starr & Oberbauer 2003). This could explain why onset of growth was observed in a larger proportion of the bulbils of Tv-32 than of Tv-40, as the main distribution area of the tetraploid cytotype is in the inland, where the snow cover is more permanent and with a longer duration as a contrast to the main distribution area of the pentapoid cytotype which is the archipelago (Kersalo & Pirinen 2009). The sporadic snow cover in the archipelago means that the populations here are subject to harsh winter conditions that could damage the plants as the snow cover is not as continuous as in the inland. This could explain why a greater proportion of the bulbils of Tv-40 start growing in the spring. The fact that a proportion of the bulbils of both cytotypes started growing in the spring may be explained by the fact that this is a mean to avoid harsh winter conditions, the proportion of bulbils that start growth in the spring can thus be related to the chance of being subject to these harsh winter conditions.

Great variation in morphology and ecology has been observed within the different cytotypes of the field garlic, especially in Central Europe (Duchoslav 2009, Duchoslav et al. 2010, Šafářová et al. 2011, Fialová & Duchoslav 2014, Duchoslav & Staňková 2015, Ježilová et al. 2015, Duchoslav et al. 2020), which would mean that the observed differences cannot only be explained by the ploidy level. In Central Europe, the different cytotypes have probably arisen several times and are thus of different origin (Duchoslav et al. 2020) which could mean that the lack of diversity within the cytotypes in the Nordics is a result of the founder effect.

The atypical population on Sveaborg

Field garlics of the cytotype Sv-32 clearly differ from the other cytotypes regarding the timing of the onset of growth. During earlier years, the bulbils from this atypical population have also differed from other tetraploid bulbils collected in Finland. The observed difference may be explained by the fact that the population might be of a completely different origin than other tetraploid populations in Finland, and would then be adapted to a different climate. Sveaborg was built in the 18th century when Finland was a part of the Swedish kingdom, this can be seen in the flora of the fortress site as several plant species introduced during the Swedish regime are still present (Vuokko 1998). There is a dock not far from the atypical population. It was used by the Swedish fleet in the 18th and in the early 19th centuries. In Finland, there are populations of field garlic that are believed to have been introduced with ballast (Hæggström & Åström 2005, Åström & Hæggström 2015). At the time that the dock at Sveaborg was in active use, the Swedish kingdom included territories in, e.g. current Germany, which could mean that the field garlic population has it origin in ballast from Central Europe. If the population is of central European origin, it likely possesses adaptations to mild winters without long cold periods. In such conditions, it would be a competitional advantage to start growth as early as possible to avoid being overshadowed in the spring. As being subject to harsh winter conditions is rather unlikely, the chance of suffering damage from cold is almost negligible and there is thus no great risk associated with onset of growth during the autumn.

The difference in the mass of the bulbils in comparison with earlier years could have affected the onset of growth, but when comparing the data of the timing of the onset of growth of this study with data from earlier experiments (Åström & Saarinen, manuscript), there does not seem to be any major differences, which means that the results of this study are representative of the cytotypes. It is worth to note that the populations Tv-32 and Tv-40 were not part of the earlier study.

To draw further conclusions about the cytotypes in the Nordics, more studies are needed with samples from a greater number of populations of a greater geographical distribution. Genetic studies could confirm the theory that all populations of the different cytotypes are of the same origin and that they express little within cytotype diversity due to the founder effect. The atypical population on Sveaborg should be included in studies with populations from Central Europe, to examine if there are any similarities.

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