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Germination ecology of Galeopsis bifida (Lamiaceae) as a pioneer species in forest succession

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TIIVISTELMÄ: PELTOPILLIKKEEN ITÄMISEKOLOGIA JA ESIINTYMINEN METSÄSUKKESSION PIONEERILAJINA

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The occurrence of *Galeopsis bifida* on clear-cut and burned forest soil and its disappearance in 4–6 years after disturbance is attributed to its germination ecology. Initially the seeds are dormant 96–100 % and remain dormant in nylon gaze bags in different types of forest humus layers at least 10 years. Dormancy is released in laboratory 1) by treatment of 100 ppm aqueous solution of GA_3, 2) by heating the dormant seeds to 40–55°C for 1–5 h and 3) by 1 % KNO_3 solution. It is concluded that conditions in clear-cut and burned areas favour germination of seeds in regard to temperature and content of nitrates in contrast to humus of closed forest vegetation where the seeds remain dormant.

Peltopillike (*Galeopsis bifida*) ilmaantuu avohakkuualoille hakkuuta seuraavina vuosina ja saattaa olla dominoiva kasvilaji, mutta häviää 4–6 vuoden kuluttua eikä esiinny suljetussa metsäkasvillisuudessa. Emokasvista varistessaan siemenet (lohkohedelmät) ovat 96–100 %:sesti lepotilassa ja säilyvät nylonharsopusseihin suljettuina metsähumuksessa lepotilaisina ainakin 10 vuotta. Siementen lepotilan päättymisen saavat laboratoriossa aikaan 1) käsittely 100 ppm gibberelliinihappoliuoksella ja 2) 1 % kaliumnitraattiliuoksella sekä 3) kuumennus 40–55°C 1–5 h. Siemenet säilyvät ilmeisesti metsähumuksessa lepotilaisina pitkiä aikoja ja avohakkuu- ja kuloalojen lämpöolosuhteet sekä humuksen korkeampi nitraattipitoisuus herättävät kasvuun ehkä koko kiertoajan humuksessa lepotilaisina säilyneet siemenet.

Keywords: *Galeopsis bifida*, germination ecology, forest succession, release of seed dormancy
ODC 182.2+176.1 *Galeopsis bifida* +181.52+161.41

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1. Introduction

The success in colonization of disturbed forest soil after fire and clear cutting depends on several types of adaptations. The pioneer plant species have either highly dispersed diaspores, deeply rooted rhizomes, by which they escape disturbance, or the seeds form a long-living dormant seed bank in forest humus (Heinselman 1981). In agricultural soils, the seed bank is of central importance in the emergency of weeds, and Finnish agricultural soils may contain up to 65 000 seeds/square meter (Paatela & Erviö 1971). The role of dormant seeds in the succession of Nordic forests has received much less attention. A well-known example is *Geranium bohemicum*, the seeds of which require heating to germinate, and the species occurs almost exclusively on recently burned forest soil to disappear in following years, but the seeds may remain in forest humus dormant for decades (Jalas 1980). Kujala (1926) suggested that certain other species occurring on burned forest soil have emerged from old dormant seeds. Rintanen (1982) has studied an occurrence of *Lotus corniculatus* on a recently ploughed forest soil in SE-Finland, and based on ^{14}C-determinations of seeds found in the soil, comes to the conclusion that the individuals have emerged from old dormant seeds. According to Granström (1982) there is considerable amount of seeds in the humus of old spruce forests in northern Sweden, and seeds of *Luzula pilosa* may form a persistent seed bank. In America, seeds of the pioneer shrub *Prunus pennsylvanica* remain dormant in the soil the whole rotation period (Marks 1974). On the other hand, seeds of Nordic forest trees, e.g. those of *Betula*, seem not to be able to survive longer periods in the soil (Granström & Fries 1985).

One of the few annual pioneer species in the succession of Finnish forests is *Galeopsis bifida*. Although it occurs as a noxious weed in agricultural soils (Mukula et al. 1969, Raatikainen & Raatikainen 1975, Raatikainen et al. 1978), and in abandoned fields after 1–3 years after cultivation (Hokkanen & Raatikainen 1977), it is found also as a native plant species on rocky outcrops and especially on larger erratic blocks (Erkamo 1980), on sea-shores and as a pioneer species in clear-cut and burned areas.

As its occurrence is largely limited to habitats free from competition, it was suggested that the germination biology plays a significant role in the distribution both in space and time. The main emphasis was laid on its occurrence as a primary colonizator of disturbed forest habitats.

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2. Observations on the occurrence of G. bifida in nature

In summers 1970–86 observations on the occurence of *Galeopsis* were made on ca. 15 clear-cut areas, ca. 20 rocky outcrops and ca. 30 erratic blocks mainly in Helsinki, Ruotsinkylä, Vesijako and Solböle experimental forests of the Finnish Forest Research Institute and in Ruotsinpyhtää archipelago (Fig. 1). Most of the places were visited during 5–8 successive years. Based on observations, the species appeared in clear-cut areas especially in more fertile habitats as isolated individuals in summer immediately after clear-cut in previous winter. In following years the species becomes sometimes a dominant plant species. Fig. 2 shows ca. 3 year old clear-cut area in Vesijako experimental forest, where *Galeopsis* was very abundant. The site was a stony *Myrtillus* type. Similarly in a drained spruce swamp in Ruotsinkylä it was very dominant after 2–3 years from logging, and the individuals attained height up to 50–80 cm. In all clear-cut areas, the species declined rapidly, the individuals became smaller and the species disappeared after 6–7 years or occurred only on places disturbed later. The species does not occur in closed forest vegetation.

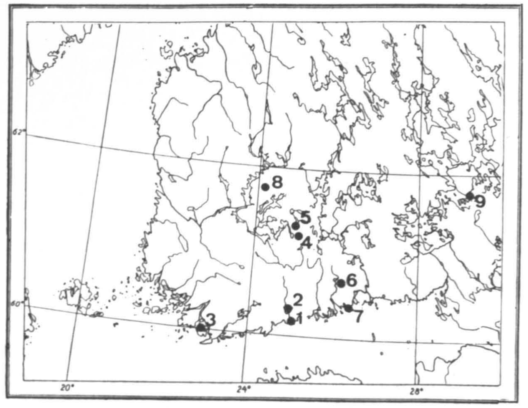

Fig. 1. Localities mentined in the text. 1: Helsinki and Vantaa, 2: Tuusula; Ruotsinkylä and Rusutjärvi, 3: Bromarv, Solböle, 4: Lammi, Evo, 5: Padasjoki, Vesijako, 6: Lapinjärvi, 7: Ruotsinpyhtää, 8: Juupajoki, Hyytiälä and 9: Punkaharju.

In Evo State forest and in Ruotsinkylä experimental forest *Galeopsis* was commonly seen on ploughed forest soil after clearcut as isolated, but rather frequent individuals. It occurred often abundantly in ditches and margins of newly build forest roads and recent landing places for timber in Vesijako 1974 and 1977, but disappeared in 1–2 years when the places were left undisturbed.

G. bifida occurs also as an early colonizator of burned soil. It was met with several times in vicinity of Helsinki and Hyytiälä as isolated individuals on burnt-over areas. In Mustavuori, city of Vantaa, it was seen in September as flowering individuals around remains of a hay barn, which was burnt at midsummer, and the seedlings grew so close that the germination had to been taken place after the fire.

On rocky outcrops and on large erratic blocks, on which the species is a permanent component of the vegetation, the numbers and size of individuals varied considerably

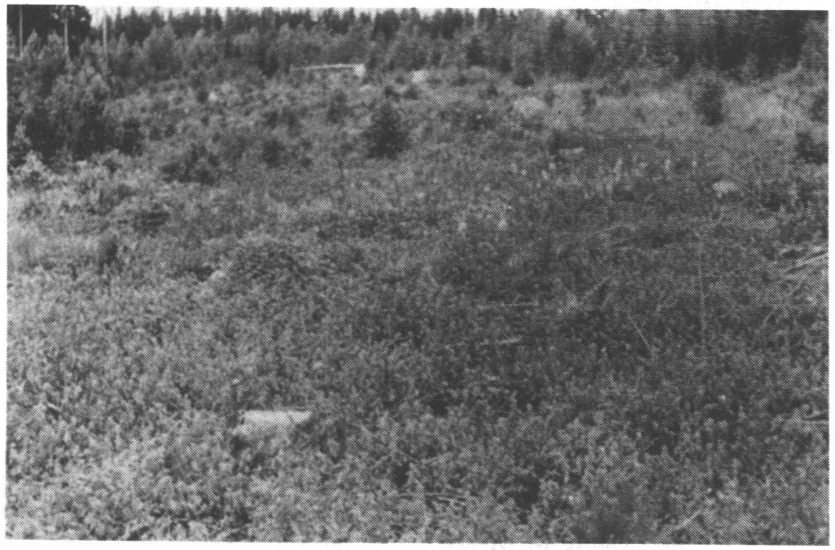

Fig. 2. An extensive and almost pure stand of *Galeopsis bifida* in a clear-cut area in Vesijako experimental forest in summer 1974. The species declined in following years and in 1978 only occasional small individuals were seen. In 1982 the species was totally absent under planted pine saplings.

between successive years. In moist summers, e.g. in 1974 the individuals were large and numerous, but in drier years smaller. In extremely dry years, mainly in 1975, on many rocky outcrops and erratic blocks no one of the seedlings in the spring reached fruiting stage due to drought. However, after drought year of 1975 the species appeared again on the same rocky outcrops and erratic blocks as earlier. In summer 1986 on several erratic blocks in late September *Galeopsis* was beginning to flower, although in normal years fruits ripen in early August. In early summer of 1986 there were long drought periods in South and Central Finland, e.g. in Helsinki from June 10 to July 10 the amount of rainfall was only 13.2 mm, but in the month of August 159.9 mm. The occurrence on such places can be explained either by originating from a dormant seed pool in humus, or from dispersal after drought from agricultural and ruderal places. For this reason the germination ecology of *Galeopsis bifida* was studied both in the field and laboratory.

3. Material and methods

3.1. Experiments with seeds of *Galeopsis bifida*

Nutlets (here called seeds) on *Galeopsis bifida* were collected in natural habitats by taking fruiting shoots into large plastic bags, allowed to stand overnight in laboratory and then gently shaken to remove seeds. The majority of the seeds were considered ripe. In collecting special care was attached to the presence of flowers, by which the species is easiest to tell apart from similar *G. speciosa*, which commonly grows in mixed stands together with *G. bifida*. The collected seeds were dried for 1 day at room temperature in laboratory and stored in a refrigerator at +5 – +6°C.

Following seed collections were used: R: Helsinki, Rastila 6679:396, Grid 27° E), roadside ditch, 1983. E: Lammi, Evo (6794:398) recently constructed roadside in forest, 1978. Rlä: Tuusula, Ruotsinkylä (6696:389), forest road border, 1979. V: Vesijako (6812:395) clear-cut area and forest roadside, 1979. K: Ruotsinpyhtää (6694:469) clear-cut area, 1984 and Vki: Helsinki, Viikki (6682:392), rocky outcrop, 1979.

3.2. Survival of *Galeopsis* seeds in forest humus

As many weed seeds remain in soil dormant extensive periods, preservation of *Galeopsis* seeds in forest humus was studied in following way. 100 seeds were placed in nylon gaze bags, ca. 7 × 7 cm, mesh size 0.4 mm, closed with nylon thread and placed into forest humus layer to a depth of 5–10 cm, to which depth seeds probably may get when they fall on the surface of humus. After 1–10 years, bags were taken into laboratory, seeds placed on filter paper in petri dishes and moistened with 100–1000 ppm gibberellic acid (GA_3) solution in order to break dormancy. Results in Table 1. Locals refer to experimetal forests of the Finnish Forest Research Institute (Fig. 1). Seeds of *Galeopsis* remained in forest humus alive at least following periods: dry pine forests (VT): 6 years (germination 67 %) mesic spruce forests (MT): 10 years (37 %), eutrophic forests of OMT-type 10 years (12 %) spruce swamps: 9 years (1–68 %), rock surface: 6 years (11 %). Evidently these values do not represent maximum preservation times, and it is possible that seeds may remain dormant in humus longer, perhaps the whole rotation time of forest stands.

3.3. Germination experiments in laboratory

Germination experiments were carried out in 10 cm glass or plastic petri dishes either on filter paper or in long-term experiments on

Table 1. Survival and germination of seeds of *G. bifida* after being buried in forest humus in nylon gaze bags for different periods. The seeds were treated in laboratory after the excavation with 100 ppm aquous solution of GA_3.

Locality and biotype	laid in humus	taken into laboratory	time in humus	germination % in laboratory after GA_3-treatment
Ruotsinkylä, protected OMT birch-spruce forest on drained swamp.	29. 9. -73	4. 7.-83	9 y 9 mo	32 left, of which 10 germinated = 10 %
Ruotsinkylä, moist dense birch-spruce swamp, leaf litter	29. 9. -73 29. 9. -73	12. 6. -82 23. 6. -82	7 y 8 mo 8 y 8 mo	36 % 27 %
Ruotsinkylä, spruce swamp in *Sphagnum girgensohnii*	29. 9. -73	4. 7. -83	9 y 9 mo	53 left, one germinated = 1 %
Ruotsinkylä, birch-spruce stand, OMT	29. 9. -73	4. 7. -83	9 y 9 mo	95 left, 68 germinated = 68 % (1000 ppm GA_3 added)
Ruotsinkylä, dense spruce plantation, in needle litter	29. 9. -73	4. 7. -83	9 y 9 mo	Bag 1:21 seeds, no germination bag 2:62 seeds left, no germination
Ruotsinkylä, old MT spruce forest under *Pleurozium*	29. 9. -73	23. 6. -82	8 y 9 mo	24 %
Ruotsinkylä, protected OMT drained spruce-birch swamp	29. 9. -73	13. 6. -84	10 y 8 mo	When taken up from humus, 8 of seeds were germinating, probably due to the fact that the bag was (due activity of rodents) near surface of the soil. In laboratory 4 additional seeds germinated, total 12 seeds viable.
Ruotsinkylä, old MT spruce stand, under carpet of *Pleurozium* and *Hylocomium*	29. 9. -73	13. 6. -84	10 y 8 mo	When taken out of humus, 4 of the seeds were germinating, 37 % germinated in laboratory
Punkaharju, protected moist mixed stand, MT	13. 8. -74	27. 7. -83	8 y 11 mo	bag 1:55 left, 20 germinated = 20 % bag 2:19
Solböle, open rock surface under a *Cladonia* plate	1. 10. -73	21. 5. -81	6 y 7 mo	11 %
Rusutjärvi, rock surface under *Cladonia*	11. 11. -74	11. 8. -80	5 y 9 mo	15 %
Rusutjärvi, *Ledum* pine bog, under *Sphagnum*	29. 12. -74	20. 6. -82	7 y 5 mo	a) 46 % b) 26 % c) 17 % (3 bags).
Ruotsinkylä, MT pine-spruce forest under *Pleurozium*	8. 11. -76	29. 6. -82	5 y 8 mo 56 %	
Ruotsinkylä, young VT pine forest, needle litter	8. 11. -76	29. 6. -82	5 y 8 mo	55 %

Table 1. cont.

Locality and biotype	laid in humus	taken into laboratory	time in humus	germination % in laboratory after GA_3-treatment
Ruotsinkylä, pole-aged pine stand, VT	8. 11. -76	4. 7. -83	6 y 8 mo	96 left, 67 %
Ruotsinkylä, moist grass-herb alder forest	9. 11. -76	11. 8. -80	3 y 9 mo	55 %
Ruotsinkylä, moist spruce swamp, under *Sphagnum girgensohnii* and *Polytrichum commune*	9. 11. -76	11. 8. -80	3 y 9 mo	41 %
Lapinjärvi, dry VT pine forest (*Calluna, Pleurozium*)	10. 11. -76	13. 8. .80	3 y 9 mo	54 %
Lapinjärvi, OMT spruce stand	10. 11. -76	29. 5. -84	7 y 6 mo	68 %
Lapinjärvi, moist dense MT spruce forest on clay soil	10. 11. -76	13. 8. -80	3 y 9 mo	71 %
Lapinjärvi, old MT spruce stand under thick *Pleurozium* moss carpet	10. 11. -76	29. 5. -84	7 y 6 mo	83 %
Ruotsinpyhtää, shady MT spruce forest, under *Pleurozium*	14. 11. -76	31. 10. -81	4 y 11 mo	a) 64 % b) 64 %
Ruotsinpyhtää, open MT spruce forest under *Pleurozium*	14. 11. -76	31. 10. -81	4 y 11 mo	52 %
Rusutjärvi, spruce swamp under *Sphagnum girgensohnii*	16. 11. -76	11. 8. -80	3 y 9 mo	68 %
Rusutjärvi, moist MT mixed forst on clay soil	16. 11. -76	11. 8. -80	3 y 9 mo	74 %
Ruotsinkylä, dense spruce swamp, in *Sphagnum girgensohnii*	16. 11. -76	4. 7. -83	6 y 7 mo	93 left, 76 germinated = 76 % (1000 ppm GA_3 added)

fine quartz sand or on Whatman GF/A glass microfibre filter in order to avoid mould contamination. The filter paper and quartz sand was kept continuously moist by adding deionized water at irregular intervals. In many cases on quartz sand the seeds remained almost free from mold interference for several years. The petri dishes were kept in a light laboratory room, and the temperature varied +22 – +26°C.

4. Results

4.1. Germination of newly collected seeds

When seeds of *G. bifida* were placed immediately after collection on moist filter paper, the germination percentage was as a rule very low, for seed source E 1.86 % (5100 seeds) and 0.00 % for K. Grime et al. (1981) reports the same for *G. tetrahit*. When placed on quartz sand in petri dishes and kept in laboratory continuously moist, they remained dormant up to 5 years. The dormant condition was indicated by treating the seeds in following ways.

4.2. The effect of nitrate

Dry seeds were immersed into 1 % KNO_3 solution for 24 hours, washed several times with deionized water and allowed to germinate. In seed source E of 900 KNO_3-treated seed germinated 13.56 % ± 2.1 (S.E.), control 4.1 ± 4.5 Seed source R: 700 seeds treated with KNO_3, germination 2.71 %, in control 5200 seeds 0.135 %. Source M: 500 treated seeds, germination was 5.2 %, in control 300 seeds 1.0 %. The germination percentage was recorded after 40–55 days.

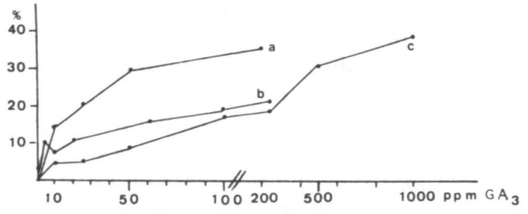

Fig. 3. The effect of gibberellic acid (GA_3) on germination of seeds of *Galeopsis bifida* in laboratory. Vertical axis: germination. a: Seed source V, b: Seed source Rlä and c: seed source VK.

4.3. The effect of gibberellic acid

Dry seeds were placed on filter paper and moistened with ca. 7 ml of different concentrations of GA_3 (Sigma G-3250). Results in Fig. 3. In an another experiment with seed source R, 10 ppm GA_3 caused germination of 31.5 % (600 seeds) and in control 5200 seeds germination was 0.135 %.

4.4. The effect of GA_3 on dormant seeds stored moist

Seeds of *Galeopsis* were kept in petri dishes on moist quartz sand in laboratory for 240 days. Then aquous solution of GA_3 was added to give a final concentration of ca. 100 ppm. Germination after treatment was in two dishes 67 and 68 %, in control untreated dishes none. In Fig. 4 a similar experiment.

Seeds (K) were kept on moist quartz sand in petri dishes in laboratory at room tempera-

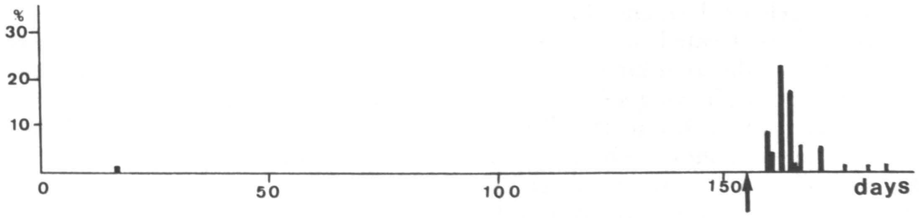

Fig. 4. The effect of GA_3 on germination of 100 dormant seeds of *G. bifidc*, which were kept on moist quarz sand in laboratory for 155 days, and then 10 ml 100 ppm solution of Ga_3 was added (arrow). Vertical axis: germination-%.

ture for 1021 days, during which time no germination occurred, although seeds were kept continuously moist with additions of deionized water. Then to the quartz sand was pipetted 5 ml of different concentrations of GA_3-solution. Then sand contained approximately 10 ml moisture. 100 ppm GA_3 solution resulted in germination of 18 %, 250 ppm 11 %, 500 ppm 34 % and 1000 ppm 45 %. In control seeds without gibberellin no germination occurred. Values are based on a single dish/concentration. It seems that the release of dormancy in aged seeds requires relatively high concentrations of GA_3.

4.5. The effect of GA_3 on dormant seeds which were kept in humus layers extended (1–9 years) periods

As described above, seeds of *Galeopsis* were placed in nylon mesh bags, and allowed to remain in forest humus for different periods. When taken into laboratory, the seeds did not germinate, but treatment of 100 ppm GA_3 solution resulted sometimes almost complete germination of the seeds, which were buried for several years in forest humus.

Based on these experiment, it is concluded that treatment with GA_3 breaks very effeciently the dormancy of the seeds of *Galeopsis* in laboratory.

4.6. Effects of forest humus, fungus extracts and tree pollen on germination of dormant seeds of *Galeopsis*

As seeds germinated readily in natural conditions in the spring, an attempt was made to investigate whether there are in forest soils substances which release dormancy like GA_3. Dormant seeds were treated with soil extracts, prepared from different kinds of forest and cultivated soils by allowing soil to stand in deionized water for 12 h and the filtrate was added to petri dishes with dormant seeds. In 30 soil samples no evidence of stimulation of germination was found. In addition, on disturbed forest soil occur regularly characteristic fungus species, e.g. *Laccaria laccata* and *Paxillus involutus* (Laiho 1970). Extracts were made from basidiocarps of both species as well as from pure culture mycelium of *Paxillus*, and added in different concentrations on seeds of *Galeopsis*, but no stimulation was found. These experiments, although not systematic, suggest that there is in forest soils scarcely any GA-like substances at least very commonly, which break the dormancy of seeds of *Galeopsis*.

Gibberellic acid is isolated from *Pinus* pollen (Kamienska et al. 1976). As considerable amounts of tree pollen is spread in the spring at the same time or later than *Galeopsis* germinates, fresh pine, spruce and alder pollen was mixed with dormant seeds in petri dishes in deionized water, but no stimulation was found.

4.7. The effect of heat treatment

100 seeds were placed on moist filter paper in petri dishes and allowed to germinate for 40–43 days. Then the petri dishes were placed in a thermostatically controlled laboratory oven, fluctuations ±1°C, and heated for ½–6 hours. Results in Table 2. Temperatures below 40°C did not have any effect on germination, but temperatures of 45–55°C for 1–5 h increased greatly the germination percentage. Temperatures over 60–65°C evidently injure the seeds based on the fact that they did not react on GA-treatment. In control dishes at room temperature germination was none.

7 petri dishes, in each 100 seeds (source R) on moist quartz sand, were kept moist by additions of deionized water for 330 days. Initial germination during first two weeks was 0.1 %, and after that none. Then the dishes were heated to 45°C for 2½ hours, resulting an average germination of 55 % in two weeks.

Seeds (source V) were kept in 3 dishes on moist quartz sand (100 seeds in each) for 1010 days in laboratory. Then seeds were heated for 1½ hours to 50°C, and the germination percentage was 38, 8 and 0 %.

Table 2. Germination of dormant seeds of *Galeopsis bifida* after heating to different temperatures for various times in Experiment 7.

Temperature	minutes 10'	15'	½ h	Duration of heat treatmet hours 1	2	3	4	5	6	8
60°	11	3	–	–	–	–	–	–	–	–
55°	11	3	3	5	–	–	–	–	–	–
50°	–	14	8	10	25	11	6	3	9	–
45°	–	0	0	1	3	19	7	13	16	
40°	–	–	0	0	0	0	1	3	1	–
35°	0	–	–	0	0	0	0	0	0	0

4.8. The effect of heating compared with GA_3-treatment

Seeds of *G. bifida* were collected in Ruotsinkylä on August 24, 1981 and 100 seeds were placed on moist quartz sand in petri dishes on following day. The sand was kept moist by additions of deionized water until April 1984, during which time no germination occurred. 2 dishes were then treated with 100 ppm solution of GA_3, resulting in germination of 85 and 81 %, two were heated to 45°C for 5 hours, resulting in 19 % and 3 % germination and three were treated both with heating 5 h at 45°C as well as by GA_3 100 ppm, resulting in germination of 91, 63 and 35 %. Result suggests that gibberellic acid releases dormancy in older seeds more effectively than heat treatment.

5. Discussion

5.1. The role of the seed bank in occurrence of *Galeopsis* in nature

The occurrence of *Galeopsis* on disturbed forest soil can be explained either by recent seed dispersal or from dormant seeds in the humus layer. The genus *Galeopsis* does not produce excessive amounts of seeds, as only 4 nutlets per flower are formed. The number of flowers varies greatly depending plant size, being approximately 10–500 and the number of seeds can be estimated to be some thousands per individum at maximum. The nutlets are large compared with most Nordic native plants, and weigh ca. 4 mg each, and thus contain considerable amount of reserve material. When the seeds of *Galeopsis* germinate, they produce a rapidly-growing seedling (average growth rate of the primary root at room temperature about 15 mm/day) and the seedling attains a height of 15–20 cm with aid of reserve materials. There are no special adaptations to long-distance dispersal. The size of the nutlets resembles to a part that of cereal grains, and earlier the grain seed has evidently been an important seed source for *Galeopsis* in the fields. Most seeds are probably strown around mother plant, although spiny calyx may be attached to animal furs (Hasselberg 1940). There are also possibilities to endozoochorical dispersal by cattle (Korsmo 1925). In addition, seeds of *Galeopsis* are eaten by granivorous birds, e.g. by finches (it is fairly common sight during autumn migration time to see a flock of finches rise from a stand of *Galeopsis*), although passerine birds crush the seeds before swallowing, thus making dispersal less probable. Finally, foodhoarding birds, mainly *Parus atricapillus*, may store seeds of *Galeopsis* in neably tree trunks (Shettleworth 1980) and thus disperse seeds.

One possible agent to dispersal to clear-cut areas is the tree-harvesting equipment and forest ploughs. In earlier days, when horses were used, hay for horses may have contained weed seeds. Nowadays logging machines and tractors may only occasionally have in wheels fixed soil from agricultural soils, thus causing dispersal (e.g. Rintanen 1982). However, one sees very seldom other weed species characteristic for agricultural soils growing together with *Galeopsis* on ploughed areas or landing places for timber.

Although the capacity of dispersal of *Galeopsis* is relatively limited compared with anemochorous species or species which produce much more diaspores, recent dispersal from agricultural areas into clear-cut areas cannot be totally excluded. However, the present experiments as well as regular occurrence on very recently disturbed and burned forest soil suggest that an alternative origin for the occurrence of species on disturbed forest habitats must be sought from the possible presence of dormant seeds in forest soil.

Although laboratory experiments are not always applicable to complex conditions in nature, on the basis of above experiments a hypothesis can be constructed to explain the colonization and survival strategy of *Galeopsis bifida*. It seems that the germination ecology is closely adaptated to colonize disturbed, competition-free habitats.

The above experiments and observations suggest that the regeneration of *Galeopsis* is based on persistent seed bank in soil (Grime 1980, type B_s). In this regard the species resembles *Prunus pennsylvanica*, which according to Marks (1974) occurs only in early stages of succession to disappear after ca. 30 years, but reappears from dormant seeds in the soil, when the forest vegetation is disturbed.

Hobbs et al. (1984) have emphasized that the storage of seeds in the soil is one of the main factors in the persistence of a species during disturbance. There are numorous reports on rapid germination of seeds after fire (Mallik et al. 1985).

5.2. The role of GA and temperature in the release of seed dormancy in forest humus

Whether GA occurs in forest soils, is not known. According to Lynch (1985), gibberellin production by other fungi than *Gibberella fugikuroi* has not been definitely established. Although it is suggested that mycorrhizal fungi produce gibberellin-like substances, their occurrence is not known in detail (Harley & Smith 1983). The present experiment with soil extracts also suggest that gibberellin-like substances do not occur at least very commonly in nature. Interesting is to note that according to Lycnh (1985) and Conzales-Lopez et al. (1986), *Azotobacter* evidently produces gibberellic acid. This bacterium is characteristic to neutral soils and in theory this bacterium could induce germination of *Galeopsis* seeds.

Although there are numerous investigations on the effect of gibberellins on seed germination, relatively few studies concern the effects of GA on aged seeds of low viability. Puls & Lamberth (1974) studied the effects of GA on ten-year-old seeds to tomato, but there was no influence on final germination percentage. Present experiments suggest that gibberellic acid may induce germination in 9–10 year old seeds of *Galeopsis*, and evidently still older, too.

Based on above experiments, in nature temperature seems to be an important factor controlling seed germination in forest soils. According to Viro (1969) in burned and clear-cut areas the temperature of uppermost soil may rise up to 36–52°C, occasionally still higher (Vaartaja 1949). In control closed stands tempereature remained around 20°C. In North Finland according to Leikola (1975) temperature of the humus layer rises in summer scarcely over +20°C in closed forest stands.

When forest soil is burned in wildfire, temperatures rise in the surface layer much higher, although the heat does not penetrate deeply into the mineral soil (Uggla 1957, Viro 1969, Ahlgren 1974).

The heat tolerance of *Galeopsis* seeds is slightly higher than values published for vegetative parts of forest plants (Flinn & Pringle 1983, Gauslaa 1984).

On the basis of temperature requirements for germination, the occurrence of *Galeopsis* on burned forest soils can be understood. *Galeopsis* seems to have been one of the most important weeds in ancient fire culture, practiced in central and eastern Finland until first world war (Heikinheimo 1915, Linkola 1921). Also Tujulin (1966) notes that "pilliheinät" (*Galeopsis* spp.) were evidently common in Kinahmi fire culture areas in North Savo. Partly the seeds may have remained in the soil dormant the whole rotation time, partly, however, they were mixed with the grain seed due to the great size of the nutlets. In addition, the cut rye or corn was dried in kilns ("riihet"), where temperature rose to 55–60°C according to Grotenfelt (1899).

The occurrence of late-flowering individuals of *Galeopsis* in September 1986 can be explained so that in early summer all seedlings were killed by drought, but the heating of dry soil during the drought induced germination of dormant seeds, which germinated later in August.

Based on this literature review, in burned areas as well as in clear-cut areas the temperature of the humus layer may rise so high that seeds of *Galeopsis* are induced to germinate. In closed stands, under a moss and litter layer, temperature remains evidently so low that germination does not take place.

Galeopsis bifida evidently has similar features in germination biology than *Geranium bohemicum*. According to Dahlgren (1928) seeds of this species require at least 35°C heat treatment to germinate and germinate well when kept 18 hours in 60°C water and remain alive after heating to 100°C (Skårman 1919, Dahlgren 1928, Jalas 1980). The seeds of *Galeopsis* seem to be considerably less tolerant to high temperatures. They do not according to present experiments survive even short heating to 100°C, but the lower limit for induction seems to be faily similar. Similarly seeds of *Geranium bohemicum* are supposed to remain in forest soils dormant for extensive periods, according to Malme (1928) ca. 30 years in a documented observation (although not verified by burial experiments) and only when the soil is heated, they germinate.

5.3. The role of nitrate in the germination of seeds fo *Galeopsis* in nature

Stimulation of seed germination by nitrate is fairly widely spread among plants and is evidently ecologically important. E.g. Freijsen et al. (1980) have found that seeds of nitrophilous *Cynoglossum officinale* germinate in nitrate-rich soils much more completely than in soils lacking nitrate. In forest soils, stimulation of germination by nitrate can be regarded as an adaptation to germinate in disturbed habitats, where competition by other plants is less severe. In closed stands, where seedlings are difficult to establish, nitrate nitrogen scarcely is accumulated, not at least in Nordic conditions (Hesselman 1937). In contrast when forest soil is disturbed, nitrification produces considerable amounts of nitrates, which are not immediately absorbed by roots (Popović 1975). According to Vitousek et al. (1979) increase in nitrification after disturbance in forest ecosystems seems to be an almost universal phenomenon. In extreme cases water in rivers coming from clear-cut areas is so badly polluted with nitrates that it is undrinkable. In North Finland, Kubin (1984) has found in the soil and running water from clear-cut areas a definite increase of nitrates. It should be noted that in incubation experiments, which partly correspond a disturbed humus layer, a considerable increase of nitrates takes as a rule place, especially in humus of more fertile site types (Tamm & Pettersson 1969). When humus in ploughing of forest soil for regeneration gets mixed with mineral soil, its nitrate content rises up to 12 times (Kubin 1984). In addition, in burned forest soil nitrification increases (Mälkönen 1982). *Galeopsis* occurs in addition sometimes in forest fertilized heavily with urea, where the rate of nitrification is also often increased (Mälkönen 1978, Martikainen 1984). Based on this review, it seems possible that increased nitrification and formation of nitrates in disturbed forest soil may at least in theory induce germination of dormant seeds in forest humus. When germination of *Galeopsis* seeds takes place, the seedling very rapidly grows in size due to large nutrient reserves in the seed.

The above observations and experiments suggest that dormant seeds of *Galeopsis* have a mechanism, possibly in the biosynthesis route of gibberellins, by which they sense in a way the prevailing conditions for germination and possibilities for further growth. The occurrence of *Galeopsis bifida* in nature in forest succession is consequently to a considerable extent determined by the germination biology.

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