Ecological investigations on Ajuga reptans, A. genevensis and their F1 hybrids

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Ecological investigations on Ajuga reptans, A. genevensis and their F_1 hybrids

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RÉSUMÉ

LÜÖND, B. & R. LÜÖND (1981). Recherches écologiques sur Ajuga reptans, *A. genevensis* et leur hybrides F_1. *Candollea* 36: 155-165. En anglais, résumé français.

Des résultats expérimentaux et des observations écologiques sur *Ajuga reptans, A. genevensis* et leurs hybrides sont présentés. *Ajuga reptans* est particulièrement bien adaptée aux prairies cultivées. *A. genevensis* demande un sol sec et lâche; elle est sensible à la compétition que lui livre la végétation des prairies riches en éléments nutritifs. La propagation végétative d'*A. genevensis* par bourgeons radicaux est plus marquée que chez *A. reptans* qui se propage par stolons, mais ce mode est mal adapté à l'environnement d'une prairie riche en éléments nutritifs. Les hybrides se comportent mieux qu'*A. genevensis* dans les prairies riches en éléments nutritifs et s'y établissent souvent. Deux expériences de compétition sont décrites et les conséquences de ces résultats sur le statut des plantes dans la nature sont discutées.

ABSTRACT

LÜÖND, B. & R. LÜÖND (1981). Ecological investigations on Ajuga reptans, *A. genevensis* and their F_1 hybrids. *Candollea* 36: 155-165. In English, French abstract.

Experimental results and observations on the ecology of *Ajuga reptans, A. genevensis* and their hybrids are presented. *Ajuga reptans* is best adapted to meadows cultivated by man. *A. genevensis* requires dry, loose soil and is sensitive to competition from the vegetation of nutrient-rich meadows. Vegetative propagation in *A. genevensis* through the means of root-buds can be much more extensive than in *A. reptans*, which spreads by runners, but it is ill-adapted to nutrient-rich meadow surroundings. Hybrids perform considerably better in nutrient-rich meadows than *A. genevensis* and often become established there. Two kinds of competition experiments are described and the bearings of their results on the situation of the plants in nature are discussed.

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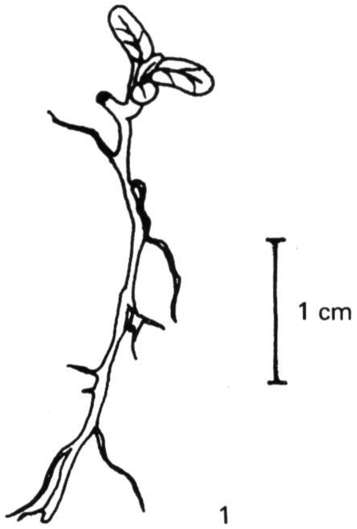
Introduction

Information in the literature about the ecology of two species of *Ajuga* native in Switzerland, *A. reptans* and *A. genevensis*, is sparse (BECKER, 1901; HEGI, 1927; RAABE, 1970; LANDOLT, 1977). *Ajuga genevensis* is mainly distributed in regions with a continental and *A. reptans* in regions with suboceanic climate, as Landolt reports. *Ajuga reptans* has a wide ecological spectrum relative to the exposition of the site. It occurs in sunny and also in shady places. *Ajuga genevensis* on the other hand requires much more light and is nearly completely restricted to south exposed and more or less inclined, dry places. Generally it can be stated that more stable sites (e.g. nutrient-rich meadows) are usually colonized by *A. reptans*; disturbed habitats (e.g. newly exposed earth by construction sites or by quarries) are often colonized by *A. genevensis*. More detailed information about the ecological preferences of the two species and their hybrids, and the mode and extent of propagation have been collected by field studies and experiments in the course of a Ph D. thesis (LÜÖND & LÜÖND, 1979).

Extent and conditions of vegetative propagation

Ajuga reptans propagates vegetatively by runners. The extent of this propagation is considerable. In an experiment with ten clones cultivated in garden beds, an average diameter of 69 cm was reached after barely two growing seasons. The number of runners that develop differs according to the conditions under which the plants are growing. In the first year of cultivation on bare soil, an average of 15.5 runners per plant was counted. In a cut meadow area this number was much smaller: only 1.9 runners per plant were produced. The number of runners produced is however not directly related to the efficiency of vegetative propagation, because the terminal rosettes of the runners often fail to root. This problem arises particularly in unused meadows and on bare places for reasons discussed in the following chapter. Beside the propagation by runners, root-buds are produced occasionally under certain conditions. In nature, root-buds appear, when a plant is damaged by treading by cattle hooves, by digging, etc. Small rosettes appear regularly at the ends of the cut root fragments near the surface (Fig. 1). The root system is more or less bell-shaped (Fig. 2). The longer roots (8-12 cm) reach the same depth as the roots of the surrounding vegetation. No buds are produced on normal undisturbed underground roots.

A. genevensis propagates vegetatively by root-buds and side rosettes growing from the base of the main shoot. The extent of this kind of vegetative propagation by root-buds has not previously been recognized in *A. genevensis*. Under favourable conditions a large number of vegetative offspring can be produced. For example a small cluster of plants in garden soil



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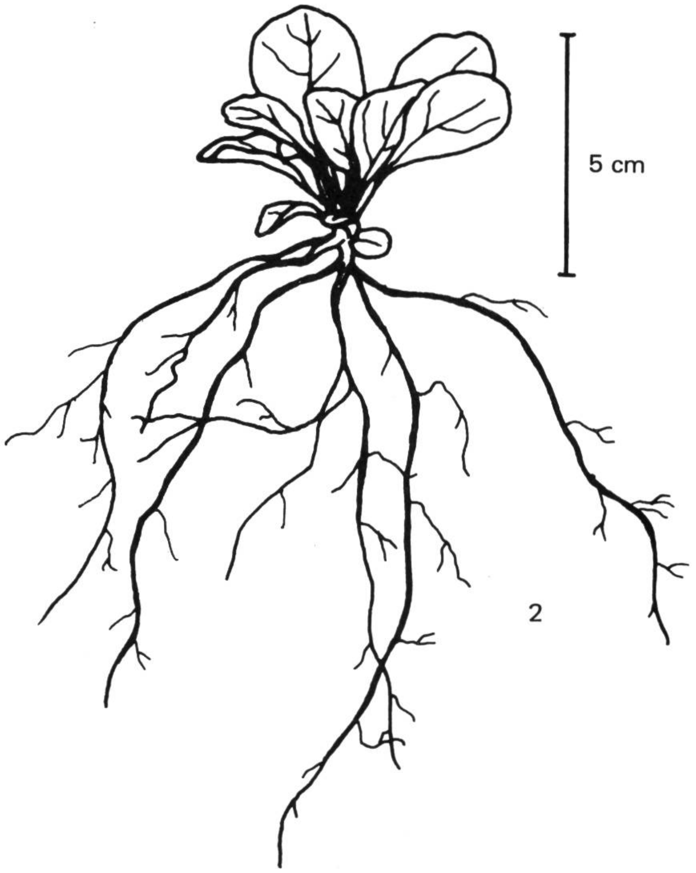

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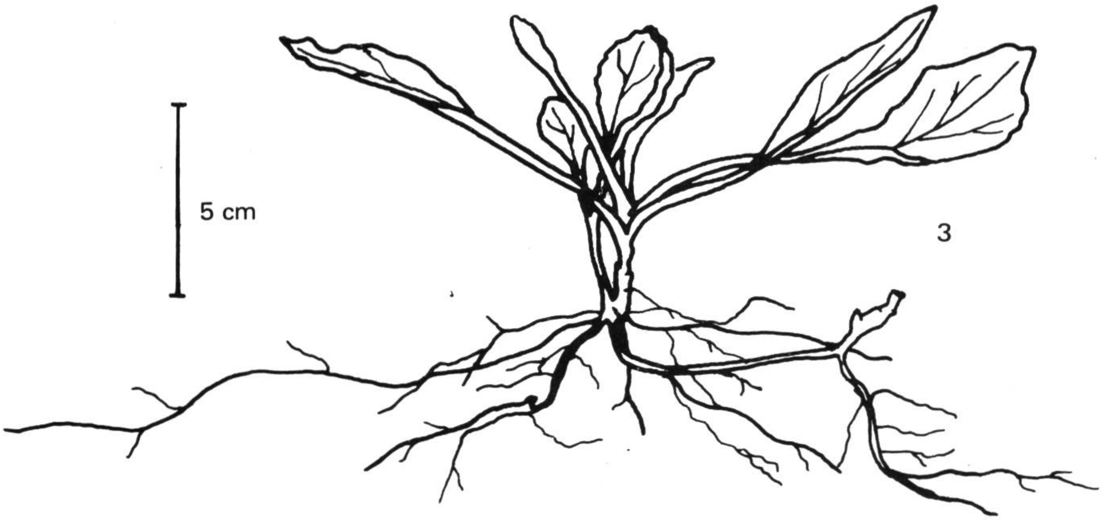

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Fig. 1. — Rosette of *A. reptans* emerging from a root fragment.
Fig. 2. — Root system of *A. reptans.*
Fig. 3. — Root system of *A. genevensis.*

produced daughter rosettes on an area of 2 m diameter after barely two growing seasons. This ability to spread could have considerable survival value for the species, because the environmental conditions usually remain favourable for only a short time in most habitats. On instable and continually changing sites like loose screes the chances of immigrating from an increasingly unfavourable habitat into a new favourable area are relatively good. The sporadic occurrence of plants of *A. genevensis* at many sites could well be connected with such evasive vegetative migrations. In compacted soil root-buds are developed when the soil cracks during drying. Bunches of root rosettes often grow out of these clefts. Experiments showed, that the growth of root-buds is not initiated by light (LÜÖND & LÜÖND, 1979), but probably due to gas diffusion in the soil. Isolated fragments of roots can produce rosettes; even fragments as short as 3 cm may develop root-buds. The rosettes grow out of the central cylinder bursting the cortex. It is by no means certain that the rosettes grow on or even reach anthesis. Marking experiments in the field showed that the majority of the rosettes do not live for more than four months. The number of rosettes reaching the flowering stage was less than 20% (LÜÖND & LÜÖND, 1979).

In contrast to *A. reptans* the roots of *A. genevensis* spread almost horizontally (Fig. 3). The roots reach a maximum depth of 5 cm. The shallow rooting and the kind of vegetative propagation connected with it make this species ill adapted to deeply and densely rooting meadow vegetation.

A comparison between the two species shows, that *A. genevensis* is capable of propagating more efficiently than *A. reptans*. For example, eight plants of *A. genevensis* planted in freshly prepared garden soil produced an average of 51 daughter rosettes per plant in the course of one growth season, whereas a group of 30 plants of *A. reptans* produced on an average only 8 daughter rosettes under the same conditions.

The rosettes that have developed from root-buds grow slower in *A. reptans* than in *A. genevensis*. It may be that this slow growth prevents the former from colonizing arable land. The rosettes from root-buds do not grow large enough between two ploughings to be able to start the next cycle of vegetative propagation. Rosettes of *A. genevensis*, on the other hand, grow quickly and develop an extensive root-system which is capable of producing root-buds within short time.

The root-system of *A. reptans* extends deeper into the soil than in *A. genevensis* and its vegetative propagation takes place outside the root-system. Therefore *A. reptans* unlike *A. genevensis* can withstand the competition in nutrient rich meadows. Observations on natural hybrids showed intermediate development of their root-systems. Their ability to grow in nutrient rich meadows is better than in *A. genevensis*. Possibly this greater tolerance against plants of nutrient rich meadows explains the existence of largely hybridized populations of *A. genevensis* in certain nutrient rich meadows.

Competition of A. reptans and A. genevensis with fertile meadows

Introduction

A. genevensis grows often, *A. reptans* less frequently at disturbed and instable sites. In the course of time the vegetation of such sites becomes more stable and the competition increases. *A. reptans* can hold its ground in this new competitive situation. The initially large populations of *A. genevensis* however dwindle drastically and often disappear completely. *A. genevensis* is never a constituent part of stable, closed vegetation on fertile soils. As *A. reptans* is frequent in meadows, it must be quite well adapted to these conditions. Regular cutting and grazing of the meadows increases the stock of populations of *A. reptans*. *Ajuga genevensis* was very rarely observed in nutrient rich meadows. It seems therefore that the two species have different competitive ability with regard to meadow plants. On the other hand, *A. reptans* is relatively uncommon on bare places in comparison to *A. genevensis*. To support these observations, experiments with both species and their hybrids were made on bare ground, in cut and not cut meadows. The experimental meadow areas chosen were typical *Arrhenatherion* associations, one in the Botanic Garden of the University of Zürich, the other at Sattel (Kt. Schwyz). Both places are south exposed. The investigated plants were autochthonous in Sattel and planted in the experimental area in Zürich. Each of the experimental areas in Zürich had an area of 1 m^2 and was planted with 30 plants of *Ajuga*. At Sattel the development of the already present populations of *A. reptans* was observed.

Results

The inflorescences of *A. reptans* in the uncut meadow were nearly three times as tall as in the cut meadow beside it. The number of pseudo-whorls however was almost the same. As in many plants, the cauline leaves which belong to the photosynthetically active part of the plant emerge from the shady part of the meadow by prolongation of the internodes. The inflorescences in tall grass therefore look looser than in short grass.

At both experimental sites (Sattel and Zürich) the number of the inflorescences decreased in the uncut areas compared with the cut ones in the course of the investigation. The seed production is therefore much larger in regularly cut meadows. But this hardly affects the extent of the sexual reproduction because most inflorescences are harvested at the end of May or the beginning of June before the fruits are ripe. For spread in cultivated meadows the plants must therefore rely on vegetative propagation. In *A. reptans* vegetative propagation is favoured by a regular cutting of the meadow. In the cut meadow the number of runners per plant is larger than in the uncut meadow, where competition for light is higher. The most important

		Cut meadow						**Bare soil**
Species		*A.r.*		*A.g.* *		*A.r.*		*A.g.* $^{+}$
Rosettes at the beginning	S	75						
	Z	30		30		30		30
				Year of observation				
		1	*2*	*1*	*2*	*1*	*2*	*1*
Established rosettes	S	99	188					
	Z	79	116	23	11	272	8	156
Number of inflorescences	S	51	74					
	Z	20	21	18	0.5	31	107	ca. 150

* average of two areas. $^{+}$ plants planted in the previous autumn

Development of A. reptans and A. genevensis in cut meadows and on bare soil.
S = Sattel; Z = Zürich

factor affecting the success of vegetative propagation is the establishment of the terminal rosettes of the runners, which is much less successful in the uncut meadow. The annual accumulation of litter from dead plant material makes it impossible for many rosettes to take root. The problem of rooting also arises for the offspring of the transplanted rosettes of *A. reptans* on bare ground. The rosettes often develop very short roots which do not enter the soil and soon wither. Growth and establishment of roots obviously require a fairly moist microclimate. This is much more easily guaranteed between transpirating meadow plants than on bare soil, the surface of which dries out within short time and no longer keeps moist the air near the soil. It takes a very wet summer like the first of the experiment (1977) for the *A. reptans* rosettes to establish successfully on bare ground. Seedlings of *A. reptans* were found only in spring and then only in small numbers in the cut meadow. On bare soil no seedlings emerged. The presence or absence of a moist microclimate is probably also the decisive factor for germination.

For the evaluation of the behaviour of the transplanted ramets of *A. genevensis* on the bare ground-area in the Botanic Garden Zürich only the first year (1977) could be considered, because the experimental plants died during the exceptionally wet weather in the late summer of 1977. A marked decrease in numbers of *A. genevensis* plants could also be observed at different natural sites. In the two years of observations the *A. genevensis* plants in the meadow areas were much weaker than those on bare ground. Generally they had only a few small rosette leaves and in both years failed to produce offshoot rosettes beside the main rosette. Only in the second year a very small number of daughter rosettes arose from root-buds. Therefore the vegetative propagation was in both years very much lower in the meadow than on bare soil (in the year that could be used for comparison). This result agrees with the observations made at natural sites. Plants with several lateral shoots and root-buds generally arise only in more or less bare places. The less luxuriant development of the mother plants in the meadows resulted in a much smaller number of inflorescences. The seed production in the meadow is therefore several times smaller than on bare ground. Seedlings appeared neither in the meadows nor on the bare ground despite the enormous seed production on bare ground. At natural sites seedlings were not frequent.

Seeds obtained from experimental crosses between *A. reptans* and *A. genevensis* were sown in March 1977. In June 1977, 30 raised F_1 seedlings were planted in bare soil and in a cut meadow. The plants grew well, but were somewhat larger on the bare ground than the meadow. In the second year of observation the production of runners was about equal in both areas with one or two runners per plant. These runners are intermediate between normal creeping runners and upright lateral shoots. At their distal ends these plagiotropic side shoots ascend slightly before producing end rosettes. The rooting of the rosettes is therefore rendered more difficult than in *A. reptans.* The following figures show the extent of the vegetative propagation of the two parental species and the F_1 in cut meadow:

Number of established rosettes at the end of two growing seasons produced by 30 initial plants:

A. reptans	116
A. genevensis	11
F_1 hybrids	43

Rosettes from root-buds in the F_1 were developed only in the bare area. Most of these plants died towards the end of the second year. In addition to the root-buds and lateral shoots the F_1 plants on bare ground also produced runners which hardly made a contribution to the propagation, because they were unable to take root and become established. As in *A. reptans* inflorescences in the F_1 do not usually develop before the second year after germination. The number of inflorescences was much larger in the bare area than in the meadow (in the second year of observation: 178 resp. 6). The seed set was much lower than in the parents. The pollen and probably also the egg cells are less fertile than in the parents.

Competition between A. reptans and A. genevensis at different proportions and different densities

Introduction and method

The two species *A. reptans* and *A. genevensis* have different demands on the environment. As was evident from the experiment described above, *A. genevensis* is much less able to compete with the vegetation of nutrient-rich meadows than *A. reptans.* An additional set of experiments was designed to investigate the behaviour of the two species in situations of direct contact. It was decided to follow the technique developed by De Wit (1960, 1961) for the investigation of the yields of agricultural crop mixtures. This method has since been applied to other combinations of species by many authors in a partly modified form (e.g. Harper & McNaughton, 1962; Tripahti & Hharper, 1973; Solbrig & Simpson, 1974).

At the start of our investigations we proceeded from the erroneous assumption that *A. reptans* propagated mainly vegetatively and *A. genevensis* sexually. The great extent of vegetative propagation of *A. genevensis* was first detected during the experiment described here.

At the end of March 1976, experimental sites were chosen in the Botanic Garden Zürich, one on a sunny terrace and the other in a shady wood. Each was divided in two times ten plots of 25 × 25 cm. These plots were delimited with corrugated plastic to a depth of ca. 23 cm. The soil mixture used was the same at both sites and consisted of loam and peat in the proportion of 3 : 1. Two rows of 5 plots for high density were planted with 16 plants each (Fig. 4). In the following two rows with low density 4 plants per plot were planted. At low and high densities two plots were planted with only *A. reptans* or only *A. genevensis.* The other three plots of each row were planted with species mixtures at proportions of 3 : 1, 1 : 1, 1 : 3. The transplanted rosettes of both species originated from natural sites. Countings of the rosette numbers were made over a two years' period at intervals of two weeks in the first year and one month in the second. For the evaluation the figures of the two replications were averaged.

Results

During the two years of observation no seedlings appeared in the experimental plots. The propagation of the transplanted rosettes resulted exclusively from runners and root-buds. Figure 5 shows in replacement diagrams the development of the rosette numbers in the different plots after one season.

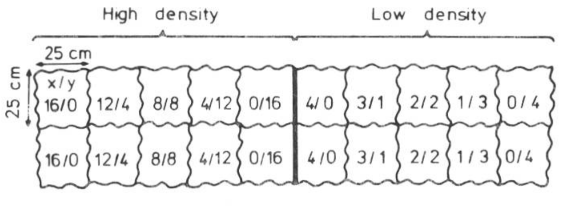

Fig. 4. — Design of replacement series experiment with *A. reptans* and *A. genevensis.* x/y = proportion of the two species.

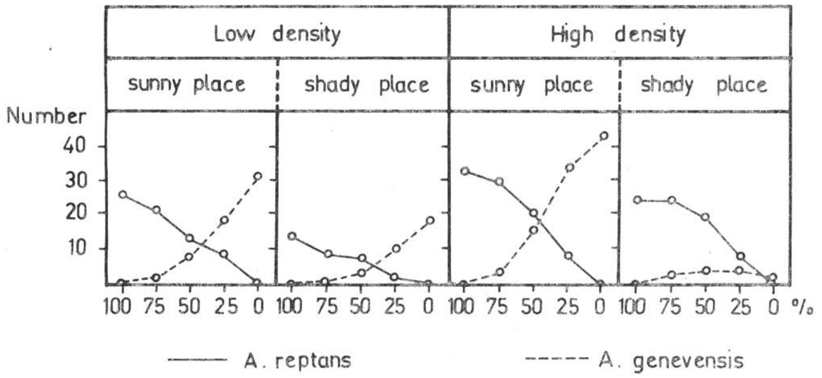

Fig. 5. — "Replacement"-diagrams of inter- and intraspecific competition after one season. Ordinate: number of the rosettes of the species; abscisse: percentage of *A. reptans* at the onset.

Short description of the results:

— Low density:

sunny place: no influence of *A. genevensis* on *A. reptans* but conversely; no intraspecific competition in either species;

shady place: propagation of *A. genevensis* in mixed culture lower than in pure culture; influence of *A. reptans* on *A. genevensis* much greater than conversely; no intraspecific competition in either species.

— High density:

sunny place: *A. genevensis* clearly impaired by *A. reptans;* slight intraspecific competition in both species;

shady place: *A. reptans* dominates strongly; *A. genevensis* grows poorly right from the start, no production of lateral and root-bud rosettes.

The reason for the general dieback of *A. genevensis* in the shady place can hardly be directly caused by inter- or intraspecific competition, but is rather due to the lack of light and the too wet soil. The experimental plots at low density got a little more sunlight. This difference was just sufficient, we suppose, to give *A. genevensis* a slightly better chance to survive at least in the areas with low competition from *A. reptans. A. reptans* had the better ability to compete under all conditions chosen for this investigation. Therefore, *A. genevensis* was in an unfavourable starting position and was replaced by *A. reptans.*

Summary and discussion

On the whole the experiments confirmed the field observations. Both *Ajuga* species have an extensive vegetative propagation. Reproduction by seeds is comparatively insignificant. Seedlings of *A. reptans* were occasionally seen in small numbers in cut meadows or protruding from moist earth cavities in spring. Almost no seedlings of *A. genevensis* were found anywhere. *Ajuga reptans* is best adapted to vegetation cultivated by man. In the long run it thrives much better in meadows than on bare soil. For an efficient propagation, the meadows must be cut or grazed. On bare ground, the rosettes of runners can rarely take root. In regularly cut meadows and in pastures, the rooting is probably facilitated by the moist microclimate. On the other hand, propagation in unharvested meadows seems to be inhibited by layers of dead vegetation and by the diminished incidence of light. In the experiments, *A. genevensis* was greatly impaired by plants of nutrient-rich meadows. In nature it does not occur in closed nutrient-rich meadows, but in poor dry meadows and especially on bare ground. In the experiment, both the vegetative and the generative reproduction were greatly restricted in the meadow. Lack of competition by other plants does not seem to be sufficient for a good growth and propagation of *A. genevensis.* On several bare sites transplanted individuals developed and propagated well at first, but later wasted away and sometimes even died. *Ajuga genevensis* requires loose and dry soil.

The meadow experiments show that *A. genevensis* is very sensitive to competition by meadow plants and *A. reptans* is not. The different competitive ability of the two species shows also in the pure and mixed culture experiments. In the long run, *A. reptans* outcompeted *A. genevensis* under the conditions of the experiments. But the results of this kind of experiment do not reflect the situation as it exists in nature. In the case of wild plants like *Ajuga,* competitive strength towards other meadow plants is immensely more important for survival than the ability to outcompete the congener. Because the two species have different ecological requirements, their contact even in sympatric populations is never so close as to produce a situation of direct competition with one another. These ecological differences are more important for the development and propagation of both species than a potential interaction between them. Not the competition between the two species limits their growth, survival and propagation, but the availability of suitable ecological conditions.

F_1 hybrids can obviously hold their ground in meadows much better than *A. genevensis.* After two growing seasons more than half of the transplanted individuals were still present. Propagation by runners in nutrient-rich meadows is not a problem for these hybrids. In this they resemble *A. reptans,* even though they did not reach the average number of runners and rooting rosettes of this species. The hybrids can support the competition of nutrient-rich meadow vegetation much better than *A. genevensis.* This holds for the individual development as well as for the power of propagation. Observation at natural sites confirmed, that natural hybrids are better adapted to nutrient-rich meadows than *A. genevensis.* Thus *Ajuga* genotypes can originate by hybridization, which are morphologically similar to *A. genevensis,* but have a greater ecological tolerance.

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