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SEXUAL REPRODUCTION IN THE CLOUDBERRY

EIRA-MAIJA RANTALA

RANTALA, E.-M. 1976. **Sexual reproduction in the cloudberry.** Ann. Agric. Fenn. 15: 295—303. (Agric. Res. Centre, Inst. Hort., SF-21500 Piikkiö, Finland).

The cloudberry (*Rubus chamaemorus* L.) spreads by means of its rhizomes, and seldom reproduces by seed. One of the reasons its seeds germinate poorly is that they have a thick, hard seed coat. After stratification under natural conditions seeds achieved over 40 % germination and after stratification in a cold chamber for 13 months 31 %.

During the first months following germination, the aerial parts of the seedling are weak and slow-growing. The main part of the seedlings energy is directed to the formation of rhizomes, which send up new shoots from the developing clone.

Index words: cloudberry, *Rubus chamaemorus* L., sexual reproduction.

The cloudberry (*Rubus chamaemorus* L.) spreads vigorously by means of rhizomes. In one growing season, a cloudberry clone consisting of numerous shoots and many metres of abundantly branching rhizomes can produce up to 50 cm of new rhizome. Vigorous vegetative propagation of this kind is much more advantageous than reproduction by seed, where success is less certain. Sexual reproduction is of very little importance for the cloudberry (ØSTGÅRD 1964, MÄKINEN and OIKARINEN 1974), except in the colonization of completely new habitats.

However, reproduction by seed has occurred and does still occur to some extent. Evidence of this is provided by the luxuriant cloudberry stands often found on bird cliffs far from the Norwegian coast (RESVOLL 1929, PAULSEN 1972),

and its occurrence on the slopes of fells, at altitudes far above the usual range of the cloudberry (RESVOLL 1929). Ravens and many sea birds have been reported to eat ripe cloudberries and excrete the seeds over wide areas (RESVOLL 1929, ØSTGÅRD 1964, PAULSEN 1972). Bears and foxes have been named as possible dispersal agents (NORMAN 1895), and, according to WATSON (1964), in Scotland the seeds are spread by grouse and ptarmigan.

Seeds from plants of the genus *Rubus* are generally difficult to germinate (JENNINGS and TULLOCH 1964), and germination percentages so far obtained in experiments with the cloudberry have been low. However, sexual reproduction is important from the point of view of research; selective breeding, designed to produce individuals with more favourable properties, is

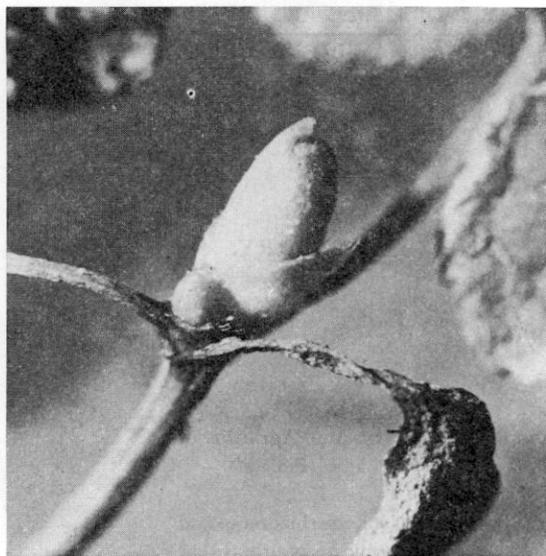


Fig. 1. Bud at base of leaf in cloudberry seedling.
Magnification $\times 13,5$

not possible unless seedlings can be obtained. The use of seed would also facilitate the creation of new cloudberry stands.

Material and methods

The material used in the germination experiments was collected in summer 1973 at Ranua, Simo, Inari and at Apukka in the rural district of Rovaniemi. In summer 1974 it was obtained from Pyhäntä, Pyhäjärvi and the Oulanka National Park in Kuusamo. The fruit was kept for 2–8 weeks in a refrigerator and the seeds were then separated in a mixer and dried at room temperature for 3–5 days. When dry, the seeds were stored in a refrigerator until taken for stratification. This was performed by covering them with a layer of damp sand and keeping them at ca. $+1^{\circ}\text{C}$ in a cold chamber. In stratification experiments still in progress a temperature of $+4^{\circ}\text{C}$ is also being used.

Instead of being stratified, seeds from Pyhäntä and Pyhäjärvi were scarified with concentrated sulphuric acid. The seeds were placed in petri dishes and sufficient acid was poured over them to cover them completely. After 1/2, 1 and 2 hours in the acid, the different batches of seeds were rinsed thoroughly under running water and sown in the usual way.

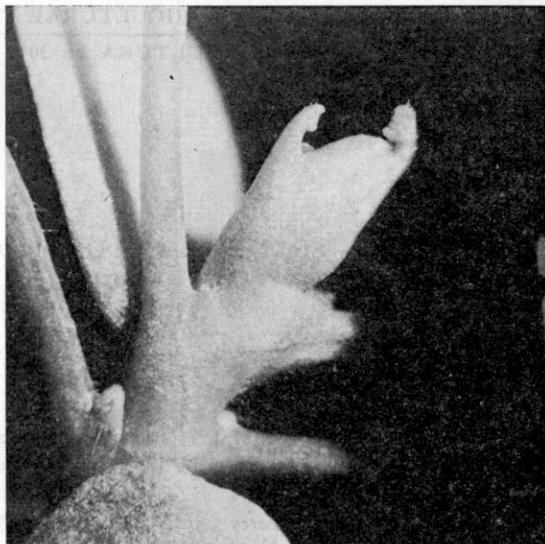


Fig. 2. Overwintering bud on seedling. Bases of cotyledons and four leaves also visible.
Magnification $\times 13,5$

The seeds were sown on the surface of a substrate of natural raw peat and covered with ca. 1 cm of sand. These seeds germinated and the seedlings raised in an automatically regulated mist propagation chamber.

Most of the stratification and germination experiments were made at the Institute of Horticulture at Piikkiö. Stratification was performed under natural conditions in an experiment at the Lapland Experimental Station at Apukka.

Structure of the fruit and seeds

The fruit of plants of genus *Rubus* consists of a collection of drupelets. The number of drupelets in cloudberry fruit ranges from 1 to 40 (SANDVED 1958, LARSSON 1969, TAYLOR 1971, ARNTZEN 1974), depending on the number of ovaries and on the success of pollination. If the weather is favourable for pollination, all the ovaries may develop into drupelets, but most often, especially if the flowering time has been cold and rainy, the fruit consists of only a few drupelets and a number of small undeveloped ovaries.

LARSSON (1969) weighed the fruits and seeds of the different *Rubus* species, and published the following table.

Species	Drupelets/fruit	Wt of single fruit, mg	Wt of single seed, mg	Seed wt/fruit, mg	Seed wt as % of fruit wt
<i>Rubus idaeus</i>	34	724	1,645	55,93	7,7
<i>R. saxatilis</i>	3	280	9,825	29,48	10,9
<i>R. stellatus</i>	29	1 934	4,228	122,61	6,3
<i>R. arcticus</i>	29	1 019	2,659	77,11	7,6
<i>R. chamaemorus</i>	18	2 490	8,168	147,02	5,9

Although the weight of the seeds in a single cloudberry was greater (147,02 mg) than the corresponding weight in any of the other species, the seeds constituted only 5,9 % of the total weight of the fruit.

The seed contained by each drupelet is composed of a seed coat surrounding a well-developed embryo. The greater part of the seed consists of two thick, succulent cotyledons, with contain the reserve food needed during germination. Between the cotyledons is a small plumule, and below it are the hypocotyl and the radicle.

The seed coat has two different layers: the inner, surrounding the embryo, is thin, soft and dark; the outer is thicker and fairly hard. The inner part of the outer layer is smoother and harder than the part forming the seed surface.

The seed coat has a weak point beside the radicle of the embryo, and here it starts to disintegrate after the seed has been stratified for some time. Similarly, stratification softens the cells of the suture encircling the seed and joining the two halves of the coat. When the seed starts to germinate, the radicle emerges through the weak point in the seed coat and the coat splits along the suture, releasing the cotyledons, which begin to turn green.

Polyembryony

The seed usually contains one embryo, but sometimes polyembryony may occur, two or more embryos being present in the same seed. Polyembryony may arise from the division of the zygote embryo, or the extra embryos may develop from nucellar cells in the embryo sac (HARTMANN and KESTER 1968). Polyembryony is by no means infrequent in the cloudberry. So far all the polyembryonic seeds I have found have contained two embryos.

The embryos were generally both well formed, but were slightly smaller than the embryos of normal seeds. In some cases one of them was much larger than the other, but the smaller embryo also appeared to be viable. Polyembryonic cloudberry seeds are usually readily distinguished from normal seeds, since in the majority the seed coat has more or less clearly defined wrinkle down the middle of the seed. Polyembryonic seeds are also often large.

The seed material collected in summer 1974 was examined and all the seeds that were large and appeared to be polyembryonic were picked up. Their seed coats were opened and the number of the embryos checked. The following numbers of seeds were found to have two embryos: 102 of 2 956 from Pyhäjärvi (3,4 %); 16 of 2 150 from Pyhäntä (0,7 %); 22 of 2 422 from Oulanka (0,9 %).

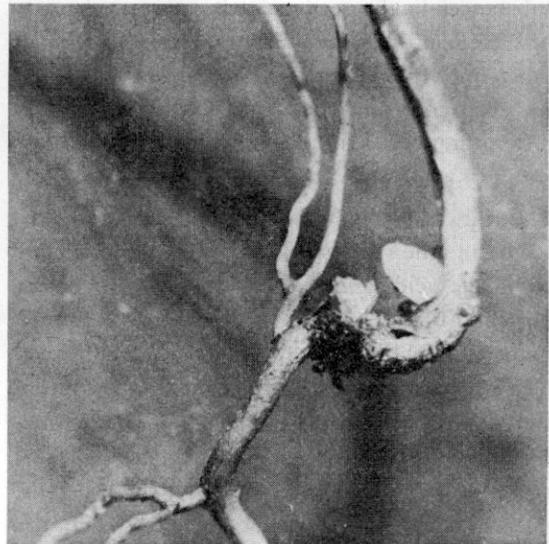


Fig. 3. Main root of seedling with the beginnings of rhizomes visible as small, white swellings. Magnification $\times 13,5$

Factors affecting germination

In many plants even under favourable conditions the seeds will not germinate immediately after being released from the parent plant. Such seeds are said to be dormant. Among the factors responsible for the state of dormancy are: and insufficiently developed embryo, an impermeable seed coat (to water or gases or perhaps both), mechanical factors preventing germination, or the absence of special temperature or light conditions. The seeds may also contain substances inhibiting germination, which gradually disappear.

All seeds need water for germination, and germination is prevented if the seed coat is not sufficiently thin or is otherwise impervious to water. In nature the seed coat is gradually softened by the activity of microbes, or by being passed through the alimentary canal of some animal. The seed coat is also weakened by changes in temperature, causing the seed to expand and contract, and by other mechanical factors. In the laboratory the coat may be softened by shaking the seeds with some abrasive substance or treating them with various chemicals. The chemicals generally used are alcohol or acids; the former dissolves waxy substances in the seed coat, but the mechanism of the effect of the acids is not quite clear. Their most important contribution may be softening the seed coat, but they may also accelerate the disappearance of inhibitory substances (MAYER and POLJAKOFF-MAYBER 1963).

JENNINGS and TULLOCH (1964) have treated seeds of the genus *Rubus* with concentrated sulphuric acid, and Professor A. Kallio of the North Minnesota Experimental Horticultural Station used 18 % hydrochloric acid with raspberry seeds (personal communication). Concentrated sulphuric acid was also used with cloudberry seeds, the treatment times being 1/2, 1 and 2 hours. None of the seeds in these batches germinated, but none of the seeds in the control group germinated either. These seeds were not stratified. The effect of concentrated sulphuric acid on empty seed coat halves was examined

by allowing them to float on the surface of sulphuric acid solution for 1/2, 1 and 2 hours. After two hours, there were small dark stains on the inside of the seed coat, indicating that the acid had penetrated the coat. The coats treated for 1/2 and 1 hour showed softening of the outer layer, but no signs that the acid had penetrated to the inside of the coat. Raspberry seeds have been treated with acid before stratification (JENNINGS and TULLOCH 1964); in this way the time required for stratification can be shortened. This method might also be suitable for cloudberry seeds, but, in the experiments undertaken so far, germination has not been obtained with the cloudberry after acid treatment alone.

Stratification

The seeds of some plants must be kept a long time in a cold, damp place before they begin to germinate; this treatment is known as stratification. After a period of stratification the seeds germinate when the temperature is raised. It has been suggested that either substances promoting germination are produced by the seeds during stratification, or the effect of inhibitory substances is decreased (LEOPOLD 1964). Changes in the enzyme activity of the seed have also been observed during cold treatment, but it is still uncertain whether these are the cause or the result of the termination of dormancy. Usually the seed coat also softens during stratification.

The stratification time and the temperature required vary with the plant species. In particular, the seeds of many of the Rosaceae have specific requirements for stratification (MAYER and POLJAKOFF-MAYBER 1963). Cloudberry seeds are reported to need a long period of stratification before they can germinate (RESVOLL 1925, LARSSON 1969, TAYLOR 1971).

In the stratification trials performed with cloudberry seeds at the Institute of Horticulture, the temperature chosen was +1°C. In the first trials the stratification times were 1, 2, 3, 4, 5, 6 and 7 months. The seeds in the control group

Table 1. Germination percentages of cloudberry seeds after different periods of stratification

Date of sowing	Stratification time, months	Germination %	Range of treatment values	No. of seeds
1974 3/4 ..	3	0	—	500
5/5 ..	4	0	—	500
3/6 ..	5	1	0—3	500
10/7 ..	6	10,4	5—15	500
2/8 ..	7	3,6	0—9	500
5/9 ..	8	2,8	0—6	500
1/10 ..	9	10,4	7—14	500
4/11 ..	10	19,6	16—25	500
2/12 ..	11	20,4	17—26	500
1975 3/1 ..	12	24,8	17—34	500
12/2 ..	13	30,8	28—36	500

were not stratified at all. Germination percentage for the whole test material of 12 000 seeds was very low — only 0,3. There were no differences in germination between the seeds stratified for different times. Evidently even seven months' stratification was not sufficiently long.

The object of the next trial was to discover at what time of the year conditions are optimal for the germination of cloudberry seeds. Seeds were sown at the beginning of each month from April 1974 to February 1975. The duration of stratification increased as the trial progressed. The stratification temperature was still +1°C.

As is seen in Table 1, the germination percentage rose as the stratification time increased. Thus the time of year does not appear to be significant for germination. The seeds were germinated in a mist propagation chamber, so the temperature and moisture did not change greatly during the course of the year. The only factor which varied widely was the intensity and spectral composition of the light, but this does not appear to affect germination as much as an increase in the length of stratification. A trial designed to elucidate what temperature is suitable for stratification and the time required is at present in progress. Preliminary results suggest that the temperature of +1°C generally used in the experiments undertaken so far is much better for stratification than +4°C. Temperatures below 0°C cannot be used, since the wet seed freezes and the embryo is destroyed at only few degrees below freezing-point.

Table 2. Germination percentages of cloudberry seeds in mire and field

Collecting locality	On mire hummocks	Between mire hummocks	Field
Apukka	2	6	22
Ranua	10	32	16
Simo	26	30	44
Inari	18	10	48
Mean	14,0	19,5	32,5

LARSSON (1969) treated *Rubus* seeds as follows: fruit collected in July—August was kept in the refrigerator at ca. 5°C until mid-September, when the seeds were separated from the fruit. The seeds were cleaned and sown in pots, which were kept at ca. 0°C for ca. 7 months. This treatment gave comparatively good results. LARSSON (1969) stresses the fact that the seeds were not allowed to dry at any stage. However, in another experiment it was found that, raspberry seeds for example germinated better if they were allowed to dry out completely before stratification (JENNINGS and TULLOCH 1964).

According to TAYLOR (1971), cloudberry seeds remain viable for fairly long; seeds dried and kept at room temperature for as long as five years have germinated after 12 months' stratification.

Stratification under natural conditions

In summer 1974 cloudberry seeds were stratified under natural conditions by being sown in a field and in mire at the Lapland Experimental Station at Apukka. The seed material collected the preceding summer from Inari, Ranua, Simo and Apukka, was dried and kept in a refrigerator at ca. +6°C until it was sown in July. In the mire the seeds were sown at a depth of ca. 5—8 cm, both on the hummocks and in the areas in between. In the field the seeds from Simo and Inari were sown at a depth of 2 cm, and those from Ranua and Apukka at a depth of 5—8 cm.

The seeds germinated better in the field than in the mire. The greater sowing depth seems to decrease germination. In the field, all the seeds had the same kind of germination substrate,

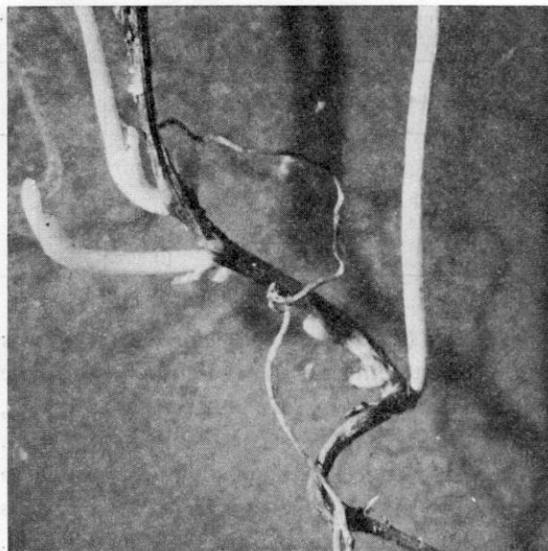


Fig. 4. Main root with rhizomes in ca. 3-month-old seedling.
Magnification $\times 13,5$

whereas in the mire conditions vary widely within a small area. For example, there can be great variation in moisture conditions in the patches between the hummocks. Thus the differences in germination between seeds collected in different localities are not necessarily due to the properties of the seed material; in the mire, germination is also affected by the heterogeneity of the germination substrate. The poor germination of the seeds sown in the mire may also be due to the great sowing depth.

In 1953—1955, Norwegian workers established five experimental fields for sowing cloudberry on the island Andøyen (ØSTGÅRD 1964). Before sowing, all vegetation was removed from the experimental fields and the soil was loosened. The seeds were sown in rows at depths of 1—2 cm and 6—7 cm. The first summer the seeds sown near the soil surface had 60—70 % germination and a year after sowing germination had risen to 80 %. The germination of the seeds sown at the greater depth was only about half as high. When both berries and seeds separated from the fruit were sown, germination results were equally good (LID et al. 1961).

The cloudberry seedlings

In the greenhouse, cotyledons appeared on the first cloudberry seedlings about one week after sowing. Germination is generally uneven; new cotyledons may appear as late as half a year after the first seeds germinate. When one month old, the seedlings already has true leaves, the first beginnings of a rhizome and an extensive root system. At the base of each leaf the seedling has an overwintering bud (RESVOLL 1929, TAYLOR 1971). According to RESVOLL, (1929), the seedling can have only three leaves, or occasionally four. However the seedlings germinated and raised in the greenhouse at the Institute of Horticulture sometimes had as many as eight leaves, and TAYLOR (1971) reports that seedlings raised by him had 4—7 leaves. The formation of so many leaves is the result of the premature development of the buds.

The seedlings grown in the greenhouse also rested during the winter. New shoots grew from the buds some months after the winter rest. In winter 1974, the leaves withered in November—December and new leaves formed in early spring. Before the beginning of the rest period, the temperature of the greenhouse was lowered from the usual $+18^{\circ}\text{C}$ to $+10^{\circ}\text{C}$. In autumn 1975, the same seedlings began their rest period in September—October, although the temperature did not change. The seedlings thus seem to have an internal rhythm which makes them begin their winter rest.

The leaves of the seedling are generally small; in three-month-old seedlings the leaves had an average length and breadth of 8,5 mm and 8,9 mm, respectively ($n = 20$). However, the seedlings had grown during the winter months, when conditions are not optimal for growth (seedlings sown on 3. 1. 1975, leaves measured 15. 4. 1975).

Growth is slow in the aerial parts of the cloudberry seedlings, the greater part of their biomass being below the ground. When the seedlings were about three months old shoots composed only 37,8 % of the total biomass. The underground biomass consisted of an

extensive root system and rhizomes. A seedling that is a few months old, with stem length of 1–2 cm and leaves ca 1 cm² in size, may have a root system extending more than 20 cm. The roots branch abundantly. The rhizomes begin to develop during the first months of the seedlings' life. They commence as small, white swellings on the root and the foot of the stem. The rhizomes elongate, giving rise to roots, and may also develop buds, from which branch new rhizomes. The bud at the apex of the rhizome produces a new aerial shoot, when the apex turns towards the surface of the soil and the bud is exposed to the light. The seedling produces rhizomes vigorously, surrounding itself with new shoots. The clone originating from a seedling of about two years may comprise 15 shoots and many new rhizomes that have not yet produced shoots (RESVOLL 1929). When a seedling has formed its first rhizomes and some new shoots, it has passed the most critical phase of its development.

The seedling apparently never flowers itself; its role is to produce new shoots, which will flower later (RESVOLL 1929). In nature, the shoots of the new clone do not flower until the 7th year after sowing, but in the greenhouse, development is somewhat quicker and flowering shoots may appear after 4 years (ØSTGÅRD 1964). In the experimental fields on the island Andøyen (cf. p. 300) the cloudberry stand had 200 flowers 9 years after sowing, only 10 % of which were pistillate. It might be expected that cloudberry stands originating from seed would have equal numbers of pistillate and staminate flowers. The reason for the abundance of the staminate flowers may be that the male plants grow more rapidly and require a shorter interval between sowing and flowering than the female plants (ØSTGÅRD 1964).

The seedling in nature

Cloudberry seedlings are seldom found in nature (RESVOLL 1925, ARNTZEN 1974). RESVOLL (1925) suggests the following reasons: the Sphagnum surface of mire is a poor substrate

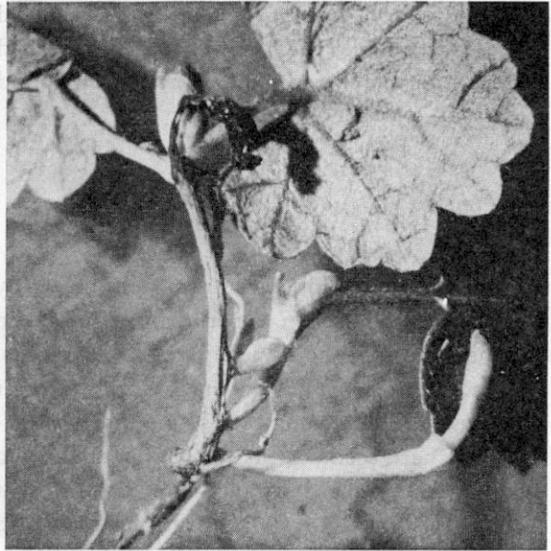


Fig. 5. Seedling showing main shoot originating from seed, new side shoot arising from rhizome, and rhizome whose upward turning apex has begun to differentiate into a new shoot.

Magnification $\times 7,5$

for germination and the hard seed coat prevents germination, or the embryo may be destroyed by frost in the autumn. In addition, good fruiting years seldom occur, so that viable seeds are not often available. LARSSON (1969) reports that northern *Rubus* species seldom germinate in nature because the seeds readily dry out. Even when seedlings do occur, they are so weak and slow-growing at first that they cannot compete for living space with the other mire plants. In nature, the seeds do not germinate the same summer the fruit was formed (TAYLOR 1971) but the following spring, after natural stratification has occurred.

At Teuravuoma in Kolari, a cloudberry seedling was found in autumn 1975 in Hanhilehto mire. The cotyledons were still present and its leaves had an average length and breadth of 5 mm. The root system was long and richly branching, and the beginnings of rhizomes were clearly discernible. The seed from which this plant had grown probably originated from the fruit yield of summer 1974 or some earlier summer. Since the cotyledons still remained, the plant must have come up in the current

growing season, but if it had grown from seed falling in summer 1975, it would not have had time to develop such abundant underground biomass.

Summary

In nature the cloudberry rarely reproduces by seed, and germination experiments undertaken in the laboratory did not give good results. Many factors may be responsible for its poor germination: e.g., poor conditions for germination, the hard seed coat, failure of the embryo to develop, or some substance in the seed that prevents germination. The very thick and hard seed coat, which is apparently one of the reasons for poor germination, can be softened with various acids. However, none of the seeds treated with concentrated sulphuric acid germinated. Another means of softening the seed

coat is stratification. Cloudberry seeds stratified for 13 months at ca. +1°C had 30,8 % germination. The best results were obtained with seeds sown in the field in which the seedlings were to grow; over 40 % of them germinated when they were sown at a depth of ca. 2 cm. A greater sowing depth seems to reduce germination. Some of the seeds sown in mire also germinated (ca. 17 %).

The aerial parts of the young seedlings grew very slowly, and the leaves formed during the first months after germination were small. At the base of each leaf is an overwintering bud, which forms a new shoot in the spring. When the seedling is only one month old, it commences vegetative reproduction, and the beginnings of the first rhizomes become visible. The greater part of the seedling's energy is directed to the development of the underground parts; when the seedling is ca. 3 months old, they form 62,2 % of its biomass.

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SELOSTUS

Hillan siemenellinen lisääntyminen

EIRA-MAIJA RANTALA

Maatalouden tutkimuskeskus¹

Hillan lisääntymistä siementen avulla tapahtuu harvoin luonnonolosuhteissa. Myöskään laboratoriossa suorituksissa idätyskokeissa ei ole saatu hyviä tuloksia. Siementen heikkoon itävyyteen voivat vaikuttaa monet eri tekijät: esimerkiksi huonot itämisolosuhteet, liian kovat siemenkuoret, alkion kehittymättömyys tai jokin itämistä estävä siemenessä oleva aine. Hillan siemenessä on hyvin paksu ja kova siemenkuori, joka todennäköisesti on eräs syy siementen heikkoon itävyyteen. Siemenkuoria voidaan pehmentää esimerkiksi erilaisten happojen avulla. Väkevällä rikkihapolla käsitellyt hillan siemenet eivät kuitenkaan ole itäneet. Myös stratifioiminen pehmentää siemenkuoria. Stratifioimalla hillan siemeniä 13 kuukautta noin +1°C:een lämpötilassa on päästy 30,8 % itävyyteen. Parhaiten ovat itäneet siemenet, jotka on kylvetty pellolle

taimien lopulliselle kasvupaikalle syksyllä. Yli 40 % tällaisista siemenistä oli itänyt, mikäli ne oli kylvetty noin 2 cm syvyyteen. Suurempi kylvösyvyys näyttää heikentävän itävyyttä. Myöskin suolle kylvetyistä siemenistä osa iti (noin 17 %).

Syntyvien siementaimien maanpäälliset osat kasvavat hyvin hitaasti. Kasvulehdet ovat ensimmäisten elinkausien aikana pieniä. Kunkin kasvulehden tyvellä on silmu, joka talvehtii ja muodostaa uuden ilmaverson keväällä. Jo kuukauden ikäisenä siementaimi aloittaa vegetatiivisen lisääntymisensä. Ensimmäiset rönsyn alut ovat tällöin havaittavissa. Suurimman osan energiastaan siementaimi käyttää maanalaisten osiensa kasvattamiseen. Noin kolmen kuukauden ikäisten siementaimien biomassasta 62,2 % on maanalaista biomassaa.

¹) Nyk. osoite: Ylioppilaskylä 17 A 10, 20500 Turku 50.

FIXATION OF AMMONIUM AND POTASSIUM APPLIED SIMULTANEOUSLY
IN FINNISH SOILS

JOUKO SIPPOLA

SIPPOLA, J. 1976. Fixation of ammonium and potassium applied simultaneously in Finnish soils. *Ann. Agric. Fenn.* 15: 304—308. (Agric. Res. Centre, Inst. Soil Sci., SF-01300 Vantaa 30, Finland).

The fixation of ammonium and potassium when added simultaneously to surface and subsoil samples representing various soil textural classes (soil types) was studied. Effects of 0,1 N HCL extraction and hydroxy-Al treatment on fixation were also investigated.

On average, from 10 to 36 % of the one milliequivalent of ammonium and potassium applied was fixed in surface soil samples. In subsoils fixation was stronger, averaging from 26 to 56 % of the amounts added.

In surface soils the ratio of fixed ammonium to fixed potassium ranged from 0,50 to 0,83. In subsoil samples the corresponding ratio was from 0,58 to 1,7. When surface soils were extracted using 0,1 N HCL, relatively more ammonium was fixed and the calculated NH_4/K -ratios were similar to those of subsoils. In subsoils pretreated with hydroxyaluminium solution, ammonium and potassium were fixed in ratios similar to those in untreated surface soils.

Index words: Ammonium and potassium fixation, aluminium interlayers.

INTRODUCTION

When ammonium and potassium are added simultaneously to soils which fix these elements it is usual that 1,5—2 times more ammonium than potassium remains nonexchangeable (NÖMMIK 1957, JANSSON and ERIKSSON 1961, DISSING NIELSEN 1971). In some acid soils, however, the reverse order of fixation has been noted (SIPPOLA et al. 1973).

The hydroxy-Al ions in the interlayers of clay minerals have been observed to affect the absorption selectivity of potassium over calcium and aluminium in vermiculite or K-depleted micas (KOZAK and HUANG 1971). It is also

known that hydrolyzed aluminium in the interlayers of vermiculite restricts the collapse of crystal spacings when saturated with potassium (SAWHNEY 1967). The presence of aluminium and its hydrolyzed forms in the interlayers of fixing minerals may explain the differences in fixation of ammonium and potassium in different soils.

The aim of this study was to test the effect of simultaneous application of ammonium and potassium on their fixation in various types of soils. Also the possible effects of aluminium on fixation were investigated.

Table 1. The means of pH_{H_2O} , organic C and clay percentage in soil types (9 samples each) with confidence limits at the 95 % level.

	Heavy clay	Silty clay	Sandy clay	Gyttja clay	Silt	Finer finesand
pH_{H_2O}						
surface soil	6,0±0,4	5,6±0,3	5,7±0,3	5,2±0,1	5,4±0,3	5,7±0,4
subsoil	6,5±0,5	6,1±0,3	6,2±0,3	4,5±0,3	5,8±0,4	5,8±0,5
Org. C %						
surface soil	3,4±1,2	4,3±1,7	3,1±0,9	6,2±1,2	3,1±1,0	3,5±1,7
subsoil	0,7±0,2	0,8±0,3	0,8±0,3	1,5±0,3	0,8±0,6	0,6±0,2
Clay %						
surface soil	70±3	47±5	35±5	46±12	25±4	14±5
subsoil	80±8	48±6	43±6	49±12	26±3	15±8

MATERIALS AND METHODS

The material used in this study included 54 surface and 54 subsoil samples, collected from various parts of Finland. Some properties of the soils, divided according to the textural classification used in Finland, are given in Table 1. Soil pH was measured in water suspension (1 : 2,5). For organic carbon a colorimetric dichromate wet digestion method was used and the content of clay was determined by a pipette method.

The simultaneous fixation of ammonium and potassium was determined by adding 25 ml of solution containing ammonium and potassium to 5 g of air-dried and powdered soil. The amount added was 1 me of each element to 100 g soil. The suspension was shaken for one hour and then 25 ml 1 N $CaCl_2$ was added and it was shaken for another hour. Then the suspension was centrifuged and clear supernatant was poured off for determinations. The ammonium not fixed was determined by steam distillation using

MgO as the base. Potassium was determined with an atomic absorption spectrophotometer. The contents of soil exchangeable ammonium and potassium were taken into account.

The effect of aluminium on fixation was first studied by adding partly neutralized $AlCl_3$ -solution to the samples, shaking them and letting them stand for a week (SAWHNEY 1967). The $AlCl_3$ -solution was prepared as follows: To $AlCl_3$ -solution, containing 5,4 g Al in 800 ml water, 110,5 N NaOH solution was added dropwise while stirring and volume was finally made to 2 l.

The effect of extraction of aluminium on fixation was tested after extracting the samples with 0,1 N HCl for 1 h (KAPOOR 1973). Afterwards, both the above treatment samples were saturated with calcium and excess salts were washed away before the addition of ammonium and potassium. All treatments were duplicated.

RESULTS AND DISCUSSION

Fixation of ammonium and potassium

About one third each of the ammonium and potassium added was fixed in heavy clay surface soils (Table 2). Fixation decreased with coarser textured soils until in the fine sands only about one tenth of the amounts added were fixed. In

surface soils fixation of potassium was much stronger than that of ammonium.

The total amount of the quantities added fixed in subsoils is almost twice that fixed in surface soils. The increase in fixing capacity in subsoils is partly due to an increase in clay

Table 2. The fixation of ammonium and potassium as me/100 g of the applied 1 me/100 g. Confidence limits at 95 % level.

	Heavy clay	Silty clay	Sandy clay	Gyttja clay	Silt	Finer finesand
Surface soils						
Ammonium	0,30 ± 0,09	0,20 ± 0,05	0,14 ± 0,04	0,13 ± 0,04	0,13 ± 0,02	0,10 ± 0,02
Potassium	0,36 ± 0,04	0,25 ± 0,03	0,21 ± 0,02	0,26 ± 0,06	0,20 ± 0,03	0,15 ± 0,03
Ratio NH ₄ /K	0,83	0,80	0,67	0,50	0,65	0,67
Subsoils						
Ammonium	0,56 ± 0,14	0,51 ± 0,23	0,40 ± 0,15	0,14 ± 0,04	0,27 ± 0,20	0,15 ± 0,14
Potassium	0,42 ± 0,06	0,30 ± 0,06	0,26 ± 0,05	0,24 ± 0,04	0,19 ± 0,05	0,16 ± 0,05
Ratio NH ₄ /K	1,33	1,70	1,54	0,58	1,42	0,94

percentage ($r = 0,50^{***}$). A higher degree of weathering and a higher content of organic matter partly restrict fixation in surface soils (KAILA 1962; FRINK 1965). In the present material the correlation coefficients between the sum of potassium and ammonium fixed, pH and content of organic carbon were $0,60^{***}$ and $-0,40^{***}$, respectively.

In subsoils, contrary to surface soils, ammonium was fixed preferentially in soils of all textural classes other than gyttja clay and finer finesand.

The ratio of fixed ammonium to fixed potassium in individual samples ranged from 0,36 to 1,9. The average ratios for soil types of subsoil samples are of same order as the ratios for

similar soils studied earlier (SIPPOLA et al. 1973). The ratios also resemble those obtained by NÖMMIK (1957) for vermiculite.

Effect of hydroxy-Al treatment

The ageing of surface soil samples in hydroxy-Al solution appears to increase fixing capacity in all soils except heavy clay (Table 3). The higher values in Table 3 compared to the values in Table 2 are due to the fact that only three surface and three subsoil samples of high fixing capacity from each soil type were taken for treatments. A comparison of the results obtained for individual surface soil samples showed that hydroxy-Al treatment had no significant effect on total

Table 3. The fixation of ammonium and potassium as me/100 g after treatment of samples with hydroxy-aluminium solution or extraction with 0,1 N HCl. Means of 3 samples in each soil type.

	Heavy clay	Silty clay	Sandy clay	Gyttja clay	Silt	Finer finesand
Al-treated						
Surface soils						
Ammonium	0,28	0,25	0,23	0,21	0,14	0,14
Potassium	0,33	0,33	0,31	0,29	0,20	0,23
Ratio NH ₄ /K	0,85	0,76	0,74	0,72	0,70	0,61
Subsoils						
Ammonium	0,27	0,22	0,25	0,22	0,12	0,14
Potassium	0,33	0,36	0,33	0,31	0,20	0,24
Ratio NH ₄ /K	0,82	0,61	0,76	0,71	0,60	0,58
Extracted with 0,1 N HCl						
Surface soils						
Ammonium	0,28	0,23	0,19	0,22	0,18	0,15
Potassium	0,19	0,17	0,15	0,16	0,09	0,07
Ratio NH ₄ /K	1,5	1,4	1,3	1,4	2,0	2,1
Subsoils						
Ammonium	0,29	0,22	0,20	0,22	0,15	0,15
Potassium	0,16	0,16	0,18	0,14	0,08	0,08
Ratio NH ₄ /K	1,8	1,4	1,1	1,6	1,9	1,9

fixation but it caused changes in the ratios of amounts fixed. Potassium was fixed in larger quantities than ammonium, as was the case with untreated samples.

In subsoils hydroxy-Al treatment decreases fixation of ammonium to below the level of that in untreated soils while potassium fixation remains almost unchanged. The ratios of fixed ammonium to fixed potassium are much lower for Al-treated than for untreated subsoils. Thus hydroxy-Al has a clear effect on fixation although the time given for interlayer formation was only one week. The OH/Al-ratio was 2.5, to ensure rapid formation of interlayers.

Effect of HCl extraction

The extraction of soils with 0.1 N HCl before adding of ammonium and potassium diminished fixation capacity quite considerably (Table 3). Also the ratio of amounts fixed changed so that ammonium was fixed in larger quantities than potassium. This change was very clear in the case of surface soil samples.

Although the samples were washed free of acid with 1 N CaCl₂ solution (pH adjusted to 7), the washing did not remove the fixation-in-

dering effect of an acid treatment, as noted for example by WIKLANDER (1950) and by NÖMMIK (1957). However, the change in ratios of fixed ammonium to fixed potassium in surface soil samples compared to untreated or Al-treated soils is clear. If adsorbed aluminium were the reason for lowered fixation in case of HCl treated samples, this should have resulted in ratios of fixed ammonium similar to those of potassium, as in the case of Al-treatment. Therefore, it may be that the 0.1 N HCl used broke down the most easily destructible crystals. This also seems likely because the largest drop in fixation occurred in clay soils.

On the other hand KAPOOR (1973) found 0.5–1.0 N HCl to be the most effective extractant of cementing material from Norwegian podzol soils, and it was not found to destroy minerals. It was on this basis also, that 0.1 N HCl was selected for the present study from several milder agents generally used for extraction of interlayer material (FRINK 1965). The amounts of aluminium extracted ranged from 42 to 191 mg/100 g soil, thus exceeding by far the amount which could be held in exchange positions. This indicates also that aluminium precipitated on soil particles, and possibly fine particle size minerals, has been dissolved.

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SELOSTUS

Maahan samanaikaisesti lisätyn ammoniumin ja kaliumin pidättyminen

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Maatalouden tutkimuskeskus

Maantutkimuslaitoksella aikaisemmin tehdyssä tutkimuksessa, jossa ammoniumia ja kaliumia lisättiin jankosta otettuihin maanäytteisiin samanaikaisesti, todettiin, että useimmissa tapauksissa ammoniumia pidättyi enemmän kuin kaliumia. Kahdessa näytteessä, joiden vesilietoksesta mitattu pH oli 5,2 ja 5,3, pidättyi kuitenkin kaliumia enemmän kuin ammoniumia. Tämän jatkotutkimuksen tarkoituksena oli selvittää laajempaan maanäyteaineistoon (taulukko 1) perustuen samanaikaisesti maahan lisätyn ammoniumin ja kaliumin pidättymistä. Lisäksi pyrittiin happouuton ja alumiinin lisäyksen avulla selvittämään pidättymissuhteiden riippuvuutta alumiinista.

Sekä muokkauskerroksesta että pohjamaasta otettuihin näytteisiin lisättiin liuosmuodossa ammoniumia ja kaliumia määrät, jotka vastasivat 280 ja 640 kiloa hehtaaria kohti (1 me/100 g kumpaakin). Muokkauskerroksen näytteisiin pidättyi maalajista riippuen 10—36 % lisä-

tyistä määristä. Aitosavet pidättivät eniten ja hienoa hie-taa olevat maat vähiten (taulukko 2). Pohjamaanäytteisiin pidättyi 26—56 % lisätyistä määristä. Pohjamaan pidätyskyky oli siten selvästi suurempi kuin muokkauskerroksesta otetun maan pidätyskyky johtuen osaksi suu-remmasta savespitoisuudesta. Muita tekijöitä, joilla ilmeisesti on osuutta suhteellisen suureen pidättymiseen pohjamaassa ovat pohjamaan orgaanisen aineksen vähyys ja muokkauskerroksen pH:ta korkeampi pH. Liejusavi-maiden sekä pinta- että pohjamaanäytteet pidättivät saman verran eikä pinta- ja pohjamaanäytteiden kohdalla ollut eroa ammoniumin ja kaliumin pidättymissuhteessa kuten muilla maalajeilla.

Näytteiden uutto 0,1 N HCl:lla johti kokonaispidätyskyvyn alentumiseen. Samalla kuitenkin ammoniumin ja kaliumin pidättymissuhteet muuttuivat siten, että pinta-maanäytteisiin kyseisiä ioneja pidättyi samassa suhteessa kuin käsittelemättömiin pohjamaanäytteisiin.

RECOVERY OF THREE TEMPERATE-CLIMATE GRASSES
FROM DROUGHT STRESS

TIMO MELA and VICTOR B. YOUNGNER

MELA, T. & YOUNGNER, V. B. 1976. Recovery of three temperate-climate grasses from drought stress. Ann. Agric. Fenn. 15: 309—315. (Agric. Res. Centre, Inst. Pl. Husb., SF-01300 Vantaa 30, Finland).

Ability to recover after drought stress of three grass species, orchardgrass (*Dactylis glomerata* L.), meadow fescue (*Festuca pratensis* Huds.) and timothy (*Phleum pratense* L.) was studied in a pot experiment. Different levels of water stress were obtained by discontinuing the watering on three dates at weekly intervals.

Water stress progressed quickest in the meadow fescue pots and slowest in the timothy pots. Drought reduced the weight of roots relatively more than the weight of tops but it had no statistically significant effect on tillering. Drought increased the percentage but decreased the absolute amounts of non-structural carbohydrates of roots in proportion to the severeness of drought stress. All plants less one survived water stress under the wilting point for 1—11 days, varying from —22 to —55 bars at the end of drought treatment.

Watering was recommenced at cutting. Timothy which was overtaken by lower water stress than the other two species recovered quickest. During the first 2—2,5 weeks of the regrowth period the dry weights of tops and within 4 weeks the dry weights of roots of timothy plants among different drought treatments equalized. The respective dry weights of the most stressed orchardgrass and meadow fescue plants still stayed reduced after 4 weeks of the regrowth period. Regrowth of tops was more vigorous than that of roots. In the beginning of regrowth the non-structural carbohydrate content and stores of roots decreased rapidly and fell lower in drought treated than in continuously watered plants. Within 4—5 weeks the content of non-structural carbohydrates was still reduced but their actual amounts in drought-treated plants had reached or surpassed their level at cutting time. The carbohydrate stores of roots of continuously watered plants were still lower than they were at cutting.

Index words: *Dactylis glomerata* L., *Festuca pratensis* Huds., *Phleum pratense* L., drought stress, recovery after drought stress, regrowth, root growth, top growth, non-structural carbohydrates.

INTRODUCTION

Rapid recovery of grasses from drought is important so that maximum benefit may be obtained from irrigation or precipitation. However, the research work done on this subject is scarce.

In most experiments the recovery of grasses has been excellent. Upon release after prolonged water stress their growth has been rapid exceeding even that of the control plants (ASHBY

and MAY 1941, LAUDE 1953). It has been concluded that a factor of great importance is good dormancy of the basal buds during drought and their rapid development into tillers after moisture becomes available (MARTIN 1930). As a result of water stress an increase in the number of tiller buds upon rewatering has been noted (ASPINALL et al. 1964).

The recovery of grasses from drought is favoured by proper management. Grasses should be grazed moderately to provide adequate food reserves for vigorous recovery after drought

(JULANDER 1945). Nitrogen fertilization decreases the percent of total non-structural carbohydrates, lowers the resistance to wilting and slows down the recovery of grasses after drought (WATSCHÉ and WADDINGTON 1975).

In the present study recovery of growth of tops and roots was investigated on three temperate-zone grass species, orchardgrass (*Dactylis glomerata* L.), meadow fescue (*Festuca pratensis* Huds.) and timothy (*Phleum pratense* L.) to clear up the prospects of irrigation of droughted pastures and grass for silage.

MATERIALS AND METHODS

The experiment was conducted at the University of California, Riverside in 1972—73. Finnish varieties of orchardgrass, meadow fescue and timothy were used, all three being called Tam-misto (Tammisto Plant Breeding Station, Finland).

The plant material was sown in a greenhouse in November 1972, three seeds per 7 cm × 7 cm peat pot. The young plants were thinned to one plant per pot. One month after germination they were moved into an illuminated refrigerator (5° C) to induce the reproductive growth phase. On 3 and 4 January 1973, the plants were transferred to 3,8 liter plastic pots filled with equal amounts by weight of a soil mixture of 60 % sandy loam and 40 % peat moss with P, K, and micronutrients. Gypsum moisture sensing blocks were placed 5 cm above the bottom of three pots in each treatment; 36 pots altogether. The total of 180 pots were arranged in a split-plot design with 4 replicates.

Greenhouse temperature maxima ranged from 20 to 28 °C, and the minima from 5 to 10 °C in January and from 10 to 15 °C in February and March. The highest temperature recorded was 31 °C, the lowest 3,5 °C. The relative humidity ranged from 40 to 60 % in the daytime and from 80 to 95 % at night.

Watering of one quarter of the plants of each species was stopped at weekly intervals on 15, 22 and 28 January while watering of one quarter of them was continued throughout the experiment (Treatments A, B, C and D respectively).

Before the start of the first drought treatment all plants were watered weekly with nutrient solution.

After all pots under the dry treatments had wilted, every plant was clipped to 5 cm. This marked the beginning of the recovery period, during which all the plants were watered equally. The starting dates of the recovery periods were 13, 15 and 17 February for timothy, meadow fescue and orchard grass, respectively.

Four plants of each species were sampled from each treatment at the start of the drought treatments, at the beginning of the recovery period, after two weeks of recovery (4 March), and after four weeks of recovery (16 March). Determinations were made of the samples of fresh and dry weights of the tops, dry weights of the roots, number of tillers and non-structural carbohydrate content of the roots. The total heights of the plants were measured at intervals of a few days. The results were tested with the analysis of variance.

Non-structural carbohydrates of grasses of temperate origin are mainly fructosans (SMITH 1968), therefore, 0,02 N H₂SO₄ was used to extract the carbohydrates from the root samples (GROTELUESCHEN and SMITH 1967). Reducing power was measured by the Schaeffer-Samogyi copperiodometric titration method described by HEINZE and MURNEEK (1940), which, according to SMITH (1969), has proved the most acceptable method. Root samples for the analysis were dried in a freeze dryer.

RESULTS AND DISCUSSION

Water Stress

Figure 1 shows the progress of drying of the soil in different drought treatments. The average number of days for which the grasses were subjected to -2 to -20 bars water stress were as follows:

	-2 bars			-20 bars		
	A	B	C	A	B	C
Orchardgrass	18	14	10	10	8	1
Meadow fescue	17	16	14	11	8	7
Timothy	15	14	7	10	7	1

The meadow fescue pots dried quickest and the timothy pots slowest. The plants stayed wilted through day at -15 to -20 bars water stress.

The drought treatment was applied during the vigorous growth of young plants. The dry

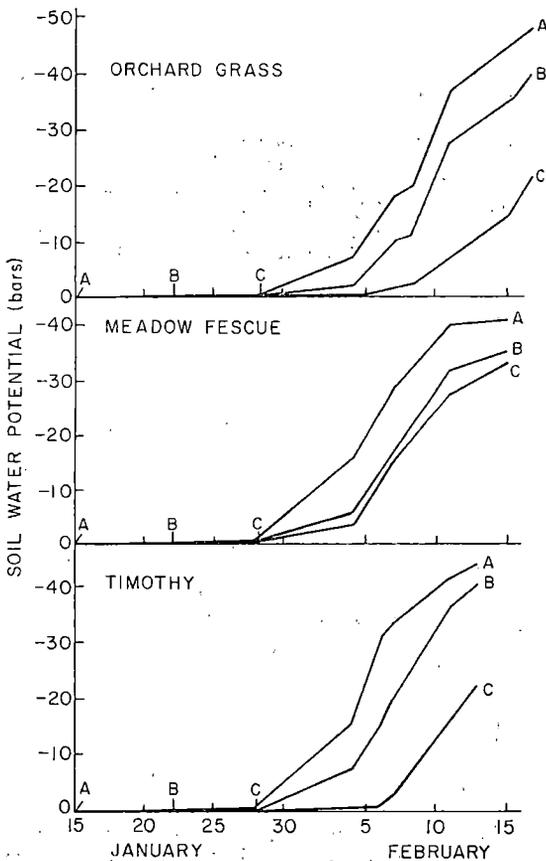


Fig. 1. The progress of drying of the soil in the drought treatments A, B, and C. Watering was stopped on 15, 22, and 28 January, respectively.

weights of the tops and roots were reduced by drought in proportion to the length of the drought treatment. (Tables 1 and 2). The inhibition of the growth of the roots by drought was relatively greater than that of the tops. At the end of the drought treatment orchardgrass had larger tops and roots than the other two species.

The average height of the grasses was reduced by less than 10% by even the most severe water stress. Drought had no statistically significant effect on tillering (Table 3). Meadow fescue formed more tillers than orchardgrass and timothy, which were approximately equal in this respect. The most severe drought killed only a few orchardgrass tillers and none of those of the other species. One orchardgrass plant died during the drought treatment. The present results are in contradiction to the observation of BROWN and BLASER (1970), which showed an increase in the number of tillers of

Table 1. Mean dry weight of tops of plants in the different drought treatments and phases of the experiment.

Treatment ¹⁾	Start of treatment g	Defoliation ²⁾ g	Regrowth	
			March 4 g	March 16 g
Orchardgrass				
A	0,48 ^{ab}	1,91 ^a	1,82 ^a	5,73 ^a
B	0,85 ^b	2,39 ^{ab}	2,76 ^b	6,13 ^a
C	1,58 ^c	2,87 ^{bc}	3,02 ^{bc}	7,13 ^b
D	—	3,49 ^c	3,58 ^c	7,01 ^b
Meadow fescue				
A	0,43 ^a	1,67 ^a	2,14 ^a	6,84 ^a
B	0,90 ^b	2,17 ^{ab}	3,12 ^b	8,30 ^b
C	1,60 ^c	2,26 ^b	3,68 ^{bc}	8,75 ^b
D	—	3,34 ^c	3,80 ^c	8,56 ^b
Timothy				
A	0,38 ^a	1,75 ^a	4,17 ^a	9,14 ^a
B	0,86 ^b	2,31 ^{ab}	4,40 ^a	9,54 ^a
C	1,88 ^c	2,45 ^b	4,51 ^a	9,51 ^a
D	—	3,20 ^c	3,97 ^a	6,91 ^b

¹⁾ Dates of the beginning of the drought treatments 15 (A), 22 (B), and 28 (C) January. D = continuously watered control.

²⁾ Dates of defoliation and the beginning of regrowth 13 (timothy) 15 (meadow fescue), and 17 (orchardgrass) February.

³⁾ Means in each column for each species by the same letter do not differ significantly at the 5% level according to Duncan's Multiple Range Test.

Table 2. Mean dry weight of roots of plants in the different drought treatments and phases of the experiment

Treatment ¹⁾	Start of treatment g	Defoliation ²⁾ g	Regrowth	
			March 4 g	March 16 g
Orchardgrass				
A	0,37 ^{a3)}	0,84 ^a	0,96 ^a	1,68 ^a
B	0,58 ^a	1,23 ^b	1,20 ^{ab}	1,89 ^a
C	1,37 ^b	1,56 ^b	1,65 ^b	2,08 ^a
D	—	3,18 ^c	2,46 ^c	2,75 ^b
Meadow fescue				
A	0,26 ^a	0,62 ^a	0,73 ^a	1,49 ^a
B	0,57 ^a	0,95 ^{ab}	1,11 ^{ab}	2,26 ^b
C	1,69 ^b	1,20 ^b	1,57 ^b	2,61 ^b
D	—	2,85 ^c	3,28 ^c	4,70 ^c
Timothy				
A	0,31 ^a	0,58 ^a	1,46 ^a	3,06 ^a
B	0,41 ^a	0,75 ^a	1,63 ^a	2,95 ^a
C	1,60 ^b	1,33 ^b	2,14 ^b	3,08 ^a
D	—	2,08 ^c	3,65 ^c	3,20 ^a

¹⁾, ²⁾, ³⁾ see Table 1.

Table 3. Mean number of tillers of plants in the different drought treatments and phases of the experiment

Treatment ¹⁾	Start of treatment no.	Defoliation ²⁾ no.	Regrowth	
			March 4 no.	March 16 no.
Orchardgrass				
A	15,8 ^{a3)}	25,8 ^a	29,5 ^a	57,5 ^a
B	19,5 ^b	29,0 ^a	33,3 ^a	61,8 ^a
C	24,8 ^c	31,5 ^a	39,3 ^a	64,0 ^a
D	—	27,8 ^a	33,8 ^a	65,8 ^a
Meadow fescue				
A	13,8 ^a	33,3 ^a	44,3 ^a	94,5 ^a
B	20,8 ^b	33,5 ^a	42,8 ^a	83,0 ^a
C	26,5 ^c	33,0 ^a	44,3 ^a	92,5 ^a
D	—	33,5 ^a	48,3 ^a	80,8 ^a
Timothy				
A	10,8 ^a	23,3 ^a	42,3 ^a	69,3 ^a
B	16,6 ^b	31,3 ^a	43,5 ^a	77,3 ^a
C	19,5 ^c	24,3 ^a	41,8 ^a	64,3 ^a
D	—	26,3 ^a	37,0 ^a	69,8 ^a

¹⁾, ²⁾, ³⁾ see Table 1.

orchardgrass at a high moisture level. On the other hand, ASPINALL et al. (1964) noted an increase in the number of tiller buds of barley as a result of water stress.

Drought increased the percentage of non-structural carbohydrates of the roots (Fig. 2). Timothy roots had the highest carbohydrate content. However, since drought inhibited root

growth, the more severe the drought treatment, the smaller were the absolute amounts of non-structural carbohydrates in the roots (Fig. 3). JULANDER (1945) and BROWN and BLASER (1970) have also found that the relative amounts of non-structural carbohydrates increase in grasses

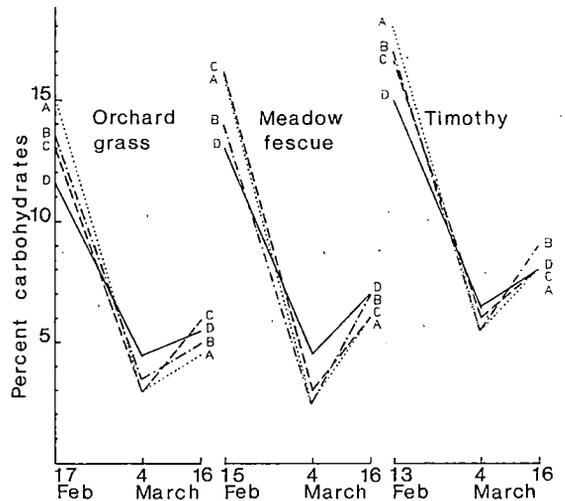


Fig. 2. Changes in percentage (dry weight) of non-structural carbohydrates in roots after defoliation. Watering in the drought treatments A, B, and C was stopped on 15, 22, and 28 January, respectively, and recommenced at the beginning of the regrowth period. D = continuously watered control.

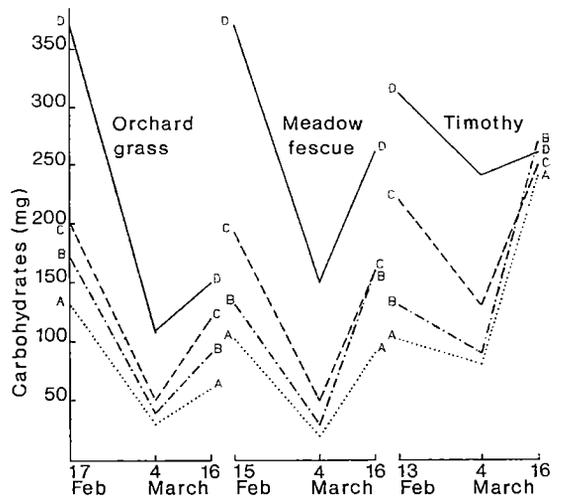


Fig. 3. Changes in quantity of non-structural carbohydrates in roots after defoliation. Watering in the drought treatments A, B, and C was stopped on 15, 22, and 28 January, respectively, and recommenced at the beginning of the regrowth period. D = continuously watered control.

under dry conditions. BLASER et al. (1966) suggests that carbohydrate accumulation in plant tissues involves a dynamic system of energy balance: (1) there is net energy loss when the amount of carbohydrates required for growth exceeds the supply from photosynthesis, (2) carbohydrate accumulates in the tissue when growth demands are low as compared with fixation by photosynthesis.

Regrowth

After the first 2—2,5 weeks of the regrowth period, effects of drought were still visible in the dry weights of the tops and roots of the orchardgrass and meadow fescue plants that had grown under dry conditions. They were still smaller than those of the plants watered continuously. Timothy which was overtaken by lower water stress than the other two species recovered quickest. Timothy plants which had suffered water stress grew very vigorously at the beginning of the regrowth period and the dry weights of their tops equaled those of the plants watered continuously. Top yields of timothy plants were larger than those of the other species.

In the following two weeks the dry weights of the tops increased 2—3 fold. Although drought-treated plants grew most at this stage and differences between the drought treatments became smaller, the effect of drought was still apparent in top and root yields of orchardgrass and meadow fescue. In contrast, there were no differences among treatments in top yields of drought-treated timothy and yields were significantly larger than those of the plants watered continuously. Top yields of timothy were highest and those of orchardgrass lowest.

Timothy roots also grew most at the beginning of the regrowth period. Their mean weight doubled in 2,5 weeks. During the same time differences among drought treatments were reduced, since roots of the plants which had been exposed to the heaviest water stress grew most. Orchardgrass and meadow fescue roots grew little in this time, but during the following

two weeks roots of all three species grew vigorously. Roots of drought-treated timothy plants reached the same weight as those of continuously watered control plants while those of drought-treated orchardgrass and meadow fescue were still smaller than those of the control plants.

In the first 2—2,5 week regrowth period the number of tillers increased 14—25 % in orchardgrass, 28—44 % in meadow fescue and 39—82 % in timothy (Table 3). During the second two-week period the ranges of the increases were 62—95 % in orchardgrass, 67—113 % in meadow fescue and 54—89 % in timothy. These figures also demonstrate the superior vigour of timothy at the beginning of regrowth. Meadow fescue produced more tillers than orchardgrass and timothy. Drought treatment had no statistically significant effect on the number of tillers formed during the regrowth period.

At the beginning of regrowth following defoliation the non-structural carbohydrate content of the roots decreased rapidly (Fig. 2). It was presumably almost at its lowest after the first regrowth period in view of the results of SMITH and SILVA (1969), which showed that decrease in the carbohydrate content continues 2—3 weeks after cutting. The carbohydrate content fell lower in drought-treated than in continuously watered plants but for all treatments it was higher in timothy than in the other grasses.

After the second regrowth period the non-structural carbohydrate content of the roots had risen but was still less than half that at the beginning of the regrowth period. Differences among drought treatments had been reduced but the carbohydrate content of timothy roots was still higher than that of the other species.

Figure 3 shows the actual amounts of non-structural carbohydrates in the roots calculated on the basis of the dry weights and the relative amounts of non-structural carbohydrates. The increase in the relative amounts of non-structural carbohydrates during the drought treatment was not enough to compensate for the decrease in root growth. The longer the drought treatment lasted the smaller were the carbohydrate

stores at the beginning of the regrowth period. During the first 2 weeks of the regrowth period, the non-structural carbohydrate stores of orchardgrass and meadow fescue roots decreased rapidly, at rates roughly equal to those of the decreases in the relative amounts, since the dry weight of the roots had increased only slightly. The carbohydrate stores of timothy roots decreased less than those of the other two species.

After 4 weeks' regrowth, the carbohydrate stores of the roots of drought-treated meadow

fescue were at about the level at which they were at cutting time but the carbohydrate stores of orchardgrass were at only about half that level. The difference in stores among drought treatments were partly leveled. The carbohydrate stores of roots of continuously watered plants were still lower than they were at cutting. Within 4—5 weeks the non-structural carbohydrate stores of timothy roots had surpassed their level at cutting time.

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Nurmiheinien toipuminen kuivuusrasituksesta

TIMO MELA

Maatalouden tutkimuskeskus

Koiranheinän, nurminadan ja timotein kykyä toipua kuivan kauden jälkeen tutkittiin astiakokeessa. Kuivuus pienensi heinäyksilöiden juurten kasvua suhteellisesti enemmän kuin lehtien ja korsien, mutta sillä ei ollut tilastollisesti merkitsevää vaikutusta versomiseen. Kuivuus lisäsi juurten liukoisten hiilihydraattien pitoisuutta, mutta pienensi hiilihydraattien kokonaismäärää juurissa, suhteessa kuivuuskäsittelyn ankaruuteen. Yhtä lukuunottamatta kaikki heinäyksilöt toipuivat kuivuusrasituksesta, jossa maan kosteus oli lakastumisrajan alapuolella 1—11 päivän ajan ja vaihteli —22:sta —50:een baariin käsittelyn lopulla.

Kuivuuskäsittelyn päätyttyä heinät niitettiin. Timotei toipui kastelun alettua nopeimmin, ja 2—2,5 viikon kuluttua kaikkien timoteiyksilöiden lehtien kuivapaino saavutti jatkuvasti kastellun verranteen tason. Sensijaan

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kuivuuskäsiteltyjen koiranheinä- ja nurminatayksilöiden lehtien ja juurten kuivapaino oli 4 viikon kuluttua kastelun aloittamisesta edelleen pienempi kuin jatkuvasti kastellun verranteen vastaavat painot.

Niiton ja kastelun aloittamisen jälkeen juurten liukoisten hiilihydraattien pitoisuus ja hiilihydraattien kokonaismäärä aleni nopeasti, kuivakäsiteltyjen heinäyksilöiden juurissa alemmalle tasolle kuin jatkuvasti kasteltujen. 4—5 viikon kuluttua hiilihydraattipitoisuus oli yhä alempi kuin niiton aikana. Kuivuuskäsiteltyjen yksilöiden juuriston hiilihydraattimäärä oli kuitenkin saavuttanut tai ohittanut niittoaikaisen tason, juuriston nopeasti kasvuaessa. Sensijaan jatkuvasti kasteltujen heinäyksilöiden juuriston hiilihydraattimäärä oli 4 viikon kuluttua edelleen huomattavasti alempi kuin niittoaikaan.

VALUE OF WHOLE OAT PLANT PELLETS IN HORSE FEEDING

VAPPU KOSSILA and GUNILLA LJUNG

KOSSILA, V. & LJUNG, G. 1976. Value of whole oat plant pellets in horse feeding. *Ann. Agric. Fenn.* 15: 316—321. (Agric. Res. Centre, Inst. Anim. Husb., 01300 Vantaa 30, Finland.)

The digestibility of whole oat plant pellets fortified with 10 % molasses and 1,5 % urea was determined on two ponies, using hay as the basic food. Digestibility, excretion, retention and balance of Ca, P, Mg, K, Na, S, Fe, Cu, Zn and Mn in ponies fed on a hay or hay-pellet diet were also estimated. The value of pellets in horses' rations was tested in a feeding trial and in a field test. Whole oat plant pellets were found to be a highly palatable, energy rich feed which had no harmful effect on the mineral balance. About 60 % of total energy intake by horses could be satisfied with the pellets. Nitrogen balance tended to be negative on a pellet diet. It is therefore advisable to provide a protein supplement when such pellets are used.

Index words: digestibility, equine, mineral balance, oat plant pellets.

Pelleting of fibrous plants facilitates feed handling and saves storage room. In cereal production much straw is obtained as a by product. Oat straw, in particular, may be used to replace a considerable part of the hay in horses' feeding, provided nutrient requirements are balanced in the diet. Straw can serve as a gut fill and the

microbes in the large intestine of the horse are capable of changing straw energy into volatile fatty acids. These, in turn, can be utilized as a energy source in the tissues of the horse. The present paper summarizes briefly the results obtained in digestibility and feeding trials on horses fed whole oat plant pellets.

MATERIAL AND METHODS

Whole oat plant was cut from the field and pressed by machine adding 10 % molasses and 1,5 % urea into 20 mm Ø pellets. These pellets were fed to two pony geldings in a digestibility-balance trial and to 22 saddle horses in a feeding and field trial.

Digestibility of whole oat plant pellet was determined by a total collection method, using timothy-dominated hay as a basic feed. The ponies were kept in specially constructed stalls, in which faeces could be separated from urine. They were fed three times daily. 30 g of calcium-

rich mineral mixture was given to the ponies at each morning feed (Table 2). They were exercised one hour daily. The digestibility-balance trial included palatability, adaptability, collection and postcollection periods each one week long.

Rate of passage of digesta through the digestive tract was determined by the chromic oxide method. Chromic oxide was mixed with a small amount of wheat bran and fed to the ponies twice daily; the feeding began 7 days before the beginning and ended 7 days after the end of the collection period. Digestibility of ordinary feed components as well as some minerals and trace elements was determined. Also excretion of the minerals and trace elements in urine and faeces, their retention levels and balances were determined during the experiment.

Whole oat plant pellets were tested on 22 saddle horses in a two-phase feeding trial and also in a less controlled field test which lasted several months. During the first phase of the

feeding trial (2 weeks) all horses received timothy-dominated hay and pellets. After two weeks, 11 of the horses were changed to a hay and oat-barley (5:1) diet. The adaptation period was one week. The rest of the experiment lasted two weeks. When the feeding trial was over each horse received 4–6 kg pellet/day in addition to oats and hay for a three-month period. The majority of the horses were the same animals as had been used in an earlier feeding experiment (KOSSILA et al. 1972) using a hay-oat diet.

Official Standardized Analytical Methods were used in analyzing feeds, faeces and urine. Sulphur was estimated according to AOAC (1965). Calcium (Ca), magnesium (Mg), phosphorus (P), sodium (Na), potassium (K), iron (Fe), copper (Cu), zinc (Zn) and manganese (Mn) were estimated by atomic absorption spectrophotometer. Chromic oxide was determined using the method of KIMURA and MILLER (1957).

RESULTS

Digestibility-balance trial

Composition of the feeds used in the digestibility-balance trial is given in Table 1. Pellets contained more fat and NFE but less crude fiber and crude protein than hay. Digestibility co-

Table 1. Composition, feeding value and digestibility coefficients (D %) of hay and oat plant pellets in the digestibility-balance trial

Component	Hay	D %	Oat plant pellet	D %
Dry matter, %	82,60	56	87,10	62
In dry matter, %				
Organic matter . .	91,11	56	93,57	67
Crude protein . . .	13,51	65	10,28	53
Crude fat	1,93	1	4,47	57
NFE	43,72	57	59,90	74
Crude fiber	31,95	54	18,92	48
Kg dry matter/fu . .	2,11		1,40	
DCP g/fu	144		86	

NFE = nitrogen free extract, fu = feed unit (1 fu = 0,7 starch unit), DCP = digestible crude protein.

efficients for pellets and hay are given in Table 1. Digestibilities of dry matter, organic matter, crude fat and NFE was higher but digestibility of crude fiber and crude protein of pellets was lower than that of hay. Nitrogen balance was +2,06 g/day on hay diet and -0,45 on hay-pellet diet. The rate of passage of the pellet-containing diet through the digestive tract was quite similar to that of the hay diet (Figs. 1 and 2). Arrows in these figures indicate the day when administration of chromic oxide ceased. From the 3rd day on, after cessation of chromic oxide administration, somewhat more chromic oxide was found in the faeces from hay diet than from hay-pellet diet.

Total daily intake, digestibility, relative amounts excreted in faeces and urine, retention and balances of minerals and trace elements on hay (I) and on hay-pellet (II) diet are given in Table 2. Total daily intake of minerals and trace elements was smaller on the hay-pellet diet than

Table 2. Mineral and trace element intake, digestibility, excretion, retention and balance in ponies fed hay (I) or hay-pellet (II) diet.

Mineral	Total daily intake		Amount received from mineral supplement I and II	Digestibility		Excretion in faeces		Excretion in urine		Retention in body		Balance	
	I	II		I	II	I	II	I	II	I	II	I	II
	g/day		g/day	%		%		%		%		g/day	
Ca	21,5	17,8	6,60	76,6	75,1	23,4	24,9	4,4	19,9	72,2	55,2	15,4	10,0
Mg	6,2	6,1	0,60	55,5	52,0	44,5	48,0	9,5	15,5	46,0	36,5	2,8	2,4
P	12,7	11,3	2,64	27,2	24,8	72,8	75,2	6,5	20,2	20,7	4,6	2,6	0,8
K	126,6	74,9	—	87,9	87,4	12,1	12,6	58,1	70,8	29,8	16,6	37,5	12,7
Na	5,1	3,0	2,10	72,1	58,2	27,9	41,8	73,0	84,4	0,9	-26,2	-0,8	0,7
S	3,7	3,7	0,03	49,8	60,8	50,2	39,2	47,7	52,2	2,1	8,6	1,0	0,3
	mg/day		mg/day	%		%		%		%		mg/day	
Fe	566	460	6	7,5	—	92,5	142,5	2,6	7,3	4,9	-49,8	29	-229
Cu	38	34	16	52,5	41,7	47,5	58,3	—	—	52,5	41,7	20	15
Zn	183	157	72	21,2	26,4	78,6	73,6	—	—	21,4	26,4	39	42
Mn	291	243	10	13,7	3,4	86,3	96,6	0,4	0,5	13,3	2,9	40	25

on a hay diet. Absolute amounts of minerals received from the mineral supplement remained constant throughout the experiment. Digestibility of different minerals and trace elements was not appreciably affected by the type of diet. Relative portions of elements excreted in faeces were similar on both types of diets with the

exception of iron, in which excretion into the faeces exceeded to a greater or lesser degree the amount of ingested iron. On the other hand, excretion of most minerals in urine was higher on hay-pellet than on hay diet. As a consequence, relative retention of most minerals was lower on diet II than on diet I.

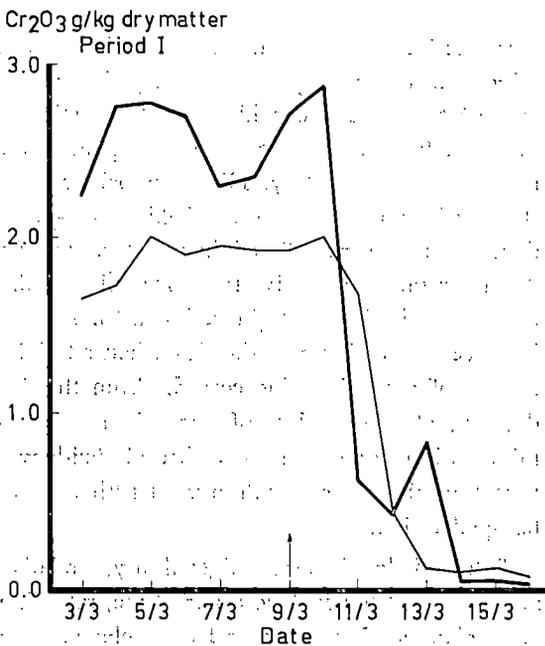


Fig. 1. Chromic oxide content in the dry matter of faeces of two ponies fed hay diet. Arrow at the base line of the figure indicates cessation of chromic oxide administration.

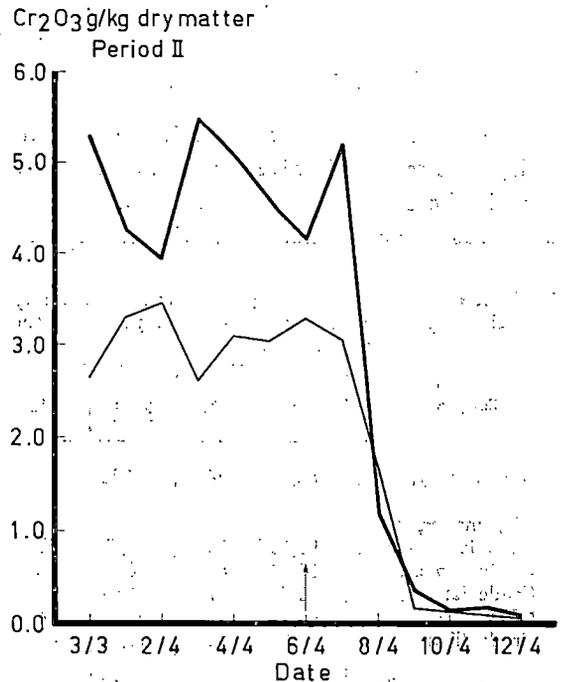


Fig. 2. Chromic oxide content in the dry matter of faeces of two ponies fed pellet-hay diet. Arrow at the base line of the figure indicates cessation of chromic oxide administration.

Mineral and trace element balances, with the exception of Na and Fe, were positive on both diets, the balances being higher on diet I than on diet II. Major portions of ingested Ca, Mg, P, Fe, Cu, Zn and Mn were excreted with faeces while K and Na were eliminated mainly via the kidneys, in urine. About one half of the ingested S was eliminated in faeces, the other half being eliminated in urine (Table 2).

Feeding trial

Results obtained from feeding trial with saddle horses are given in Tables 3 and 4. Composition

Table 3. Composition of feeds used in the feeding trial of riding horses

Component	Hay	Oat plant pellet	Oat-barley grain
Dry matter, %	77,70	92,17	87,29
In dry matter, %			
Organic matter	90,14	93,54	97,11
Crude protein	10,08	10,05	11,54
Crude fat	1,43	4,29	4,54
NFE	40,67	60,11	72,39
Crude fiber	37,96	19,09	8,64
Kg dry matter/fu	2,57	1,34	0,90
DCP g/fu	114	85	79

of feeds are given in Table 3, and average amounts of the feeds consumed by the two groups of horses during the two experimental periods are given in Table 4. Hay used in this experiment contained considerably more crude fiber but less crude protein compared to hay used in the digestibility-balance trial, 2,57 kg dry matter of hay in the feeding trial was required to furnish one feed unit (Table 3). Correspondingly, 2,11 kg dry matter of hay used in the digestibility-balance trial was required to furnish one feed unit (Table 1). The results of the feeding trial indicated that 60% of the total energy intake of horses could be furnished easily by the pellets. Horses were very fond of the pellets.

Total daily dry matter intake of horses weighing 525 kg was close on 10 kg, on average, and about 45% of this intake was obtained from pellets. Dry matter intake could be reduced and energy intake increased by substituting oat-barley meal in place of pellets, which were more bulky (1,34 kg dry matter/fu) than grain mixture (0,90 kg dry matter/fu). Horses in group 1 were ridden about 2,05 h/day and those in group 2 about 1,65 h/day on average.

Table 4. Feed consumption of riding horses during pellet feeding trial

Group	Feed	Period I			Period II		
		Average daily intake/horse			Average daily intake/horse		
		kg DM	fu	DCP g	kg DM	fu	DCP g
1	Hay	5,23	2,04	232	5,89	2,29	261
	Pellet	4,60	3,33	286	—	—	—
	Grain	—	—	—	3,73	3,85	304
	Supplements	0,18	0,18	21	0,30	0,27	31
	Total daily intake	10,10	5,55	539	9,92	6,41	596
2	Hay	5,64	2,19	250	5,37	2,09	239
	Pellet	4,80	3,47	298	5,02	3,74	318
	Supplements	0,24	0,22	30	0,42	0,41	54
	Total daily intake	10,68	5,88	578	10,81	6,24	611

Mean live weight of the horses in each group was 526 kg. Group 1 worked 2,05 and group 2 1,65 h/day on the average during the trial.

DISCUSSION

A number of digestibility studies have been done on horses (ref. OLSSON and RUUDVERE 1955). According to HINTZ (1969), digestibilities

of organic substance, crude protein, and fiber of feeds rich in fiber are 51, 56 and 38% while those of feeds poor in fiber are 79, 75 and 24%

respectively in horse. In the light of these coefficients, the feeds (hay and whole oat plant pellets fortified with molasses and urea) tested in the present study were digested rather well (Table 1). Pellets contained oat seeds and molasses which have high feeding value and can be utilized well by the equine.

The effect of pelleting on the digestibility of feeds has been studied, among others by HINTZ and LOY (1966) and HAENLEIN et al. (1966). They found that the digestibility of fiber decreases when feed is pelleted. This is due to the more rapid passage of the feed through the digestive tract of the horse. According to MEYER (1974) pelleting may decrease the digestibility of fiber up to 15%. On the other hand, ERIKSSON's (1973) investigation failed to reveal any significant effects of pelleting hay on the digestibility of organic substance, crude protein, crude fat, NFE or crude fiber. In this study whole oat plant pellet had higher nutritive value than hay, this difference being due to variation in the chemical composition rather than the physical properties of the two feeds. Feed passes through the digestive tract on the equine within 2—4 days (LENKETT 1932, OLSSON et al. 1949, HINTZ and LOY 1966, VANDER NOOT et al. 1967). The major portion, i.e. over 50% of ingested feed, leaves the digestive tract within 30—40 hours. The results of the present study agree well with earlier studies (see Figs. 1 and 2).

The digestibility and retention of minerals and trace elements depends, among other things on the type of rations on the concentration and chemical characteristics of these substances in the feeds and on the mineral and vitamin status of the animals. Not very much is known yet on the digestibility and fate of these substances in the equine. Moreover, mineral and trace element requirement figures for horses are largely based on the assumption that these requirements are similar to those of pigs or beef cattle. The ponies in the present study had not received extra minerals before the experiment began. It is therefore possible

that they were deficient in some elements. This may be reflected in digestibility, excretion, retention and balance values (Table 3).

According to SCHRYVER and HINTZ (1972) horses need 0,35% Ca and 0,25% P in their diet. Ca/P of the diet should lie between 1,4 and 2,0. Mg requirement in horses is 13—14 mg Mg/kg live weight (HINTZ and SCHRYVER 1972). According to MEYER (1974), horses weighing 300—400 kg and doing light work require the following amounts of minerals and trace elements daily: Ca 14—18 g, P 10 g, Mg 5 g, Na 10 g, Fe 40 ppm, Cu 5—8 ppm, Zn 30—50 ppm and Mn 20 ppm. K and S requirements are not given. The Mn requirement figure seems too low. In the present study the live weight of the ponies was close to 300 kg (270 kg). According to the above figures, the ponies in the present study received sufficient Ca, P, Mg and trace elements (see Table 2). Their diet was, however, short of Na and, apparently for this reason Na balance become negative (Table 2). During the pellet feeding period negative Fe balance was noted. This phenomenon need not necessarily be alarming, since Fe is one of those elements which may easily give inexplicable results due to contaminations or large amounts of insoluble Fe compound in the feeds derived from the soil during harvesting. K and S requirements of the equine is not known. Results of the present study suggest that about 1 g S/100 kg live weight is sufficient to maintain positive S balance in mature, lightly exercised pony geldings. In the present study experimental diets contained considerably more K than was sufficient to maintain a slightly positive K balance (Table 2).

Nitrogen balance tended to be negative on rations containing pellets. A similar phenomenon has been found when straw pellets were fed to sheep (KOSSILA 1975). Average size saddle horses (530—550 kg live weight) consume about 10 kg dry matter daily (KOSSILA et al. 1972) on medium heavy work. The results of the present study agree well with this earlier study, in which the horse material was largely the same.

CONCLUSIONS

Whole oat plant pellets fortified with urea and molasses were found to be suitable feed for ponies and horses. The nutritive value of pellets was higher than that of timothy hay. Pellets had no harmful effects on the digestive functions or on digestion, excretion and retention of minerals and trace elements. Moreover, pellets were highly palatable and could thus be recommended for feeding to adult sports horses doing medium

heavy work. Nitrogen balance tended to be negative when straw was introduced into the diet. It seems justified to recommend the use of protein-rich supplement in the diet of horses if straw pellets are fed to them over an extended period. This is especially true in the case of rapidly growing young horses, sports horses under intensive training, lactating mares and breeding stallions.

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SELOSTUS

Kaurakopsien ravintoarvosta hevosilla

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Maatalouden tutkimuskeskus

Melassia ja ureaa sisältävien kaurakopsien sulavuus ja tyypitase määritettiin kahdella ponilla. Perusrehussa käytettiin heinää. Samalla määritettiin kalsiumin, fosforin, magnesiumin, kaliumin, natriumin, rikin, raudan, kuparin, sinkin ja mangaanin pidättyminen, sulavuus ja erittyminen sotaan ja virtsaan. Tutkimus osoitti, että kaurakopsi oli maittava, energiarikas rehu, joka ei vaikuttanut

haitallisesti kivennäistasapainoon. Hevosilla suoritetuissa ruokintakokeissa noin 60 % syödyistä kokonaisenergiämäärästä pystyttiin helposti korvaamaan kaurakopseilla. N-tase oli lievästi negatiivinen kopsiruokinnalla. Tästä syystä suositellaan käytettäväksi valkuaisväkirehua kopsiruokinnan ohella.

EFFECT OF PHYSICAL STRESS ON THE PULSE AND RESPIRATION RATES AND BLOOD COMPOSITION OF RIDING HORSES AND TROTTERS

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The physical condition of 51 riding horses and 31 trotters was measured by tests specially designed for the purpose. The tests included measurements of pulse and respiration rates at rest, during the test, at peak stress and 10 min after cessation of the physical stress as well as determinations of blood Hb, Hc, lactate, plasma lactate, glucose, Ca, Mg, inorganic P, K, Na, Fe, Cu, Zn and total protein at rest and at peak stress. Trotters had higher pulse and respiration rates than riding horses. Physical stress caused more marked changes in the blood levels and plasma constituents in the trotters than in riding horses. Speed during the test affected blood composition. The faster the horses moved during the 30—40 min stage of the test the higher were their Hb, Hc, glucose, Na, Cu, total protein and lactate. Degree of training, weather conditions, age, sex and disposition influenced the results. It is concluded that during constant test conditions, with standardized speed and load, welltrained, healthy, balanced and fast horses are likely to show less changes in blood composition than untrained, unbalanced, slow or sick horses.

Index words: blood composition, equine, respiration, physical stress.

A good sports horse should be able to do sufficient muscle work with relatively little effort in order to fulfil its task satisfactorily. Different types of tests have been used for measuring physical condition in horses. In this paper two types of test are described, one for riding horses and the other for trotters. The results of tests made on 51 riding horses and 33 trotters are presented.

Material and methods

The following test patterns were used to study changes in the pulse and respiration rates and blood composition of the horses:

Riding horses: Trotting with rider at a speed of 230 m/min for the first 35 minutes. Galloping at a speed of 340 m/min for the next 5 minutes. Walking without rider for the next 10 minutes. Flat ground.

Trotters: Ordinary trotting at a speed of 375 m/min for the first 35 minutes. Fast trotting at an average speed of 455 m/min for the next 2 minutes. The race course was flat. Standing in the stable for the next 10 minutes.

Pulse and respiration rates of the horses were measured simultaneously by two persons with a stethoscope. Values at rest (0 min values) were obtained while horses were standing in the stable. Working values were obtained at 10, 20, 30 and 40 min (trotters 37

min) stages during the test. Return values were measured at the 50 min stage (trotters 47 min). Similar time factors are, however, used for both trotters and riding horses when presenting the results of the tests here.

Blood samples were taken from the v. jugularis into heparinized test tubes at 0 min and at 40 min stages during the tests. Hemoglobin (Hb) was determined by the cyanmethemoglobin method, blood and plasma lactic acid by HOHORST's (1962) enzymatic method and plasma total protein by REINHOLD's et al. (1950) modification of KINGSLEY's (1939) method. Hematocrit was estimated by the microcapillary method. Plasma glucose was determined using NELSON's (1944) method and inorganic phosphorus (P) according to TAUSSKY and SHORR's (1953) method. Calcium (Ca), magnesium (Mg), sodium (Na), potassium (K), iron (Fe), copper (Cu) and zinc (Zn) in plasma were estimates with an atomic absorption spectrophotometer.

Age, sex, breed, height at withers and previous training intensity (0 = untrained, 4 = intensively trained) were recorded for each horse. Total weight of the rider and saddle was recorded for riding horses. 9 to 12 horses were tested in

one day. Three groups of riding horses were tested indoors and two groups outdoors. Trotters were tested outdoors, all at the same race course. Weather conditions were recorded (0 = -5°C raining . . . , 9 = +15°C sunshine).

Results

Mean pulse and respiration rates at different stages of the tests are given in Table 1. Blood and plasma composition at rest and at peak stress are in Table 2. Results in Tables 1 and 2

Table 1. Pulse and respiration rates of riding horses and trotters at different stages of physical stress test

Time min	Riding horses (N=51)		Trotters (N=33)	
	\bar{X}	SD	\bar{X}	SD
Pulse rates, n/min				
0	36,74	± 5,71	37,18	± 6,05
10	62,10	± 8,24	97,93	± 19,76
20	67,37	± 8,30	103,21	± 21,36
30	68,57	± 9,03	100,91	± 23,95
40	87,14	± 9,70	111,27	± 17,27
50	49,59	± 5,98	60,12	± 9,90
Respiration rates, n/min				
0	18,39	± 15,14	19,27	± 5,79
10	44,41	± 16,63	74,21	± 22,47
20	49,04	± 16,81	77,64	± 19,55
30	53,39	± 16,33	78,12	± 18,56
40	70,08	± 17,62	82,97	± 20,05
50	31,18	± 9,56	44,52	± 17,67

Table 2. Blood and plasma constituents of riding horses and trotters at rest (I) and after physical stress (II)

	Riding horses (N=51)		Trotters (N=33)	
	I $\bar{X} \pm SD$	II $\bar{X} \pm SD$	I $\bar{X} \pm SD$	II $\bar{X} \pm SD$
Hb, g/100 ml	12,81 ± 1,42	15,97 ± 1,16***	13,74 ± 2,01	18,82 ± 1,62***
Hc, %	35,71 ± 4,03	42,91 ± 3,04***	39,19 ± 5,36	52,13 ± 4,18***
Gluc., mg %	100,29 ± 9,72	93,99 ± 12,38	102,29 ± 12,51	104,72 ± 15,89
Ca, mg %	12,64 ± 0,57	12,09 ± 0,41**	11,76 ± 0,70	11,17 ± 0,67**
Mg, »	1,80 ± 0,14	1,72 ± 0,14	1,82 ± 0,31	1,77 ± 0,31
P, »	3,33 ± 0,48	3,82 ± 0,45**	3,45 ± 0,66	4,31 ± 0,80***
K, »	17,20 ± 1,97	19,16 ± 0,95*	17,92 ± 2,39	19,08 ± 1,24*
Na, »	315,53 ± 13,50	316,55 ± 13,86	318,03 ± 7,45	320,09 ± 7,94
Fe, µg %	116,75 ± 24,99	135,98 ± 27,98*	130,15 ± 47,82	168,12 ± 58,21*
Cu, »	79,02 ± 13,66	82,02 ± 15,80	80,55 ± 10,67	83,73 ± 10,16
Zn, »	50,39 ± 14,11	47,78 ± 13,95	57,60 ± 13,10	54,76 ± 9,87
Tot. prot. g %	6,87 ¹⁾	7,13 ¹⁾	6,96 ± 0,46	7,70 ± 0,39
Bl. lact., mg %	7,04 ¹⁾	11,72 ¹⁾ **	9,63 ± 1,62	32,53 ± 24,51***
Pl. lact., mg %	6,58 ²⁾	11,42 ²⁾ **	9,05 ± 1,78	39,70 ± 33,48***

N = number of tested horses, \bar{X} = mean, SD = standard deviation, I = resting values, II = values at peak stress. ** P < 0,01, * P < 0,005, *** P < 0,001, ¹⁾ N = 30, ²⁾ N = 39.

demonstrate that at rest and at peak stress, average pulse and respiration rates as well as most blood and plasma values were higher in trotters than in riding horses.

During physical stress, pulse and respiration rates of the trotters rose higher than those of riding horses. On the other hand, the peak stress values were higher and normalization rates after stress were faster in riding horses than in trotters.

As a whole, physical stress caused more marked changes in the levels of blood and plasma constituents in the trotters than in riding horses (Table 2): Hb rose 24,7*** and 37,0*** %, Hc rose 20,3*** and 33,0*** %, blood lactate rose 66** and 237*** % and plasma lactate 73,6** and 339*** % respectively. Plasma glucose changed -6,3 and +2,4 %, Ca decreased -4,4 and -5,0 %, Mg decreased -4,4 and 2,8 %, plasma inorganic P elevated 14,7*** and 24,9*** %, K rose 11,4* and 6,5* %. Na changed very little, 0,3 and 0,7 %, Fe rose 16,5* and

29,2* %, Cu rose slightly 3,8 and 4,0 % and Zn decreased slightly -5,2 and -4,9 %.

At peak stress, pulse rate correlated significantly and positively with Hb***, Hc***, glucose***, Na*, Fe*, total protein* as well as blood and plasma lactic acid*** levels. Significant negative correlation was found between pulse rate and plasma Ca**. Respiration rate correlated significantly and positively with Hb*, Hc*, glucose***, Na*, Zn* and lactic acid levels.

Speed during the test affected the horses' blood composition. The faster the horses moved during the 30-40 min of the test the higher their Hc***, Hb***, glucose***, Na***, Cu***, total protein*** and lactic acid*** levels, but the lower their Ca* level at peak stress.

Weight of the rider plus saddle had hardly any effect on pulse or respiration rates or on blood composition in riding horses.

Degree of training mainly affected respiration rate, which decreased with increasing training intensity. Correspondingly, plasma phosphorus

Table 3. Effect of age of trotters on the blood composition and pulse and respiration rates at rest and at stress peak

No. of cases	Trotters			
	At rest		At stress peak	
	Growing 16	Fullgrown 17	Growing 16	Fullgrown 17
Hb, g/100 ml	12,59 ^b	14,84 ^a	17,96 ^b	19,64 ^a
Hc, %	36,06 ^b	42,14 ^a	50,02 ^b	54,11 ^a
Glucose, mg %	108 ^a	97 ^b	106	104
Ca, mg %	11,51 ^b	11,99 ^a	10,93 ^b	11,40 ^a
Mg, »	1,71	1,93	1,66	1,87
P, »	3,61	3,27	4,41	4,22
K, mg %	17,72	18,10	19,11	19,06
Na, »	319	317	318	321
Fe, µg %	124	136	159	176
Cu, »	82	80	85	83
Zn, »	58	57	53	56
Tot. prot., g %	6,89	7,02	7,69	7,70
Bl. lact., mg %	9,16	10,07	31,29	33,70
Pl. lact., »	8,94	9,15	38,16	41,15
Pulse, n/min	38,00	36,41	112,13	110,47
Respir., n/min	19,63	18,94	84,88	81,18
Tempo ¹⁾	—	—	130	127
Training degree	—	—	2,69	3,00
Weather	—	—	4,94	4,24

a > b = P < 0,005, ¹⁾ Tempo sec/1 000 m during the last two minutes of the test.

increased while lactate level decreased markedly in the samples taken at peak stress.

Weather conditions influenced the results. With increasing ambient temperature, pulse rate increased significantly in riding horses during the test. Also Hb, Hc, glucose, Na, Cu, total protein and lactate levels decreased either slightly or significantly at peak stress when the weather became warmer.

Mean age of the 84 horses tested was 6,6 years. The trotters were younger than the riding horses. It was possible to compare the blood composition of growing (2—4 years-old) trotters to that of full grown (5 years-old or older) trotters (Table 3). Such a comparison was not possible in the riding horses since only one of them was less than 5 years old. Compared to growing trotters, fullgrown trotters had significantly higher Hb, Hc and Ca values both at rest and at peak stress while plasma glucose level was lower at rest (Table 3).

Sex of the horses affected blood composition somewhat (Table 4). The majority of the riding horses tested were geldings. These had significantly lower Hb values at rest and at peak stress than mares. On the other hand, mares had more Mg but less P in their plasma than geldings. Sex did not significantly affect the blood composition of trotters (Table 4). Trotter geldings had blood values similar to those of riding horse geldings. Disposition particularly affected Hb and Hc values and pulse and respiration rates of the horses at rest (Table 5). At peak stress there were no significant differences in these parameters.

Discussion

The higher blood values of trotters at rest compared to riding horses (Table 2) may be due to differences in sex (Table 4), age (Table 3) and season of the year. Trotters were tested in late fall while most riding horses were tested during winter and spring.

The blood values obtained in this study agree well with earlier works (SCHLAM 1963, SOLIMAN and NADIM 1966, PERSSON 1967, KNUDSEN et al.

1971, KOSSILA et al. 1972, MÜLLER-REH 1972, RAJAKOSKI et al. 1972).

More marked changes in the blood composition and the pulse and respiration rates of trotters compared to riding horses are probably due to more strenuous physical stress of the trotters during the test. Both types of sports-horses were sweating heavily during the last phase of the test.

The method of measuring pulse and respiration rates in this study can be considered conventional. Repeatability was satisfactory, and this was demonstrated, for instance, by steady working values (Table 1) during the test. Pulse and respiration rates obtained by this method are considerably lower than actual rates during physical exercise. The reason for this is that when a horse is stopped to measure pulse and respiration, these rates have time to slow down during the first 5 seconds after stopping. Less marked elevation in the pulse rates of trotters at peak stress may be partly due to the fact that these values levelled off somewhat when the trotters were run into the nearby stable where the measurements at the 40 min stage were made and blood samples taken. Trotters were so hot after the test run that they could not be held quiet on the race track. Also, when working values are low, the peak stress is likely to be more prominent than when working values are high.

According to STEEL (1963) and LASKOW (1965), well trained sportshorses should have Hb of 14—16 g/100 ml at rest and about 19 g at peak stress. Untrained horses have Hb of 11—12 at rest. Reasonably high Hb and Hc values are desirable for effective oxygen transport and glucose oxidation in the muscles during physical stress. PERSSON (1967) found that there is a linear relationship between the Hb level and speed during the test. He also noted that the performance of trotters correlated positively with total circulating Hb. Very high Hb and Hc values are undesirable and can be considered a sign of pathological hemoconcentration, which is often found in older trotter stallions. In this study, one stallion had Hb of 21,9 and Hc 61 %

Table 4. Effect of sex of riding horses and trotters on the blood values and pulse and respiration rates at rest and at stress peak

No. of cases	Riding horses						Trotters						
	At rest			At stress peak			At rest			At stress peak			
	M	G	S	M	G	S	M	G	S	M	G	S	
	9	41	41	9	41	16	13	4	16	13	4	16	
Hb, g/100 ml	14,37 ^a	12,48 ^b	15,70 ^b	16,97 ^a	12,07	11,71	13,96	12,28	11,48	11,87	18,91	17,34	19,13
Hc, %	40,20	34,77	42,29	45,13	1,70	1,79	39,10	35,18	1,86	1,84	51,95	47,88	53,33
Gluc, mg %	99	100	96	87	3,89 ^a	3,62	109	105	3,45	3,33	108	108	101
Ca, mg %	12,63	12,63	12,07	12,14	1,78	1,70	11,71	11,48	1,86	1,84	11,25	11,43	11,05
Mg, »	1,86 ^a	1,78 ^b	1,70	1,78	3,43 ^b	3,62	1,79	1,86	1,78	1,84	1,78	1,87	1,75
P, »	3,00	3,40	3,89 ^a	3,43 ^b	19,12	19,34	3,62	3,45	3,45	3,33	4,48	4,38	4,16
K, mg %	16,35 ^b	17,40 ^a	19,12	19,34	318	318	18,00	14,38	18,74	18,74	19,18	18,24	19,22
Na, »	311	316	318	311	139	139	318	324	324	316	322	322	319
Fe, µg %	104	119	139	124	82	82	133	119	80	131	166	156	173
Cu, »	76	79	82	78	48	48	86	80	77	77	89	83	80
Zn, »	44	52	48	42	—	—	56	50	50	61	52	54	57
Tot. prot., g %	—	—	—	—	—	—	6,92	6,87	7,01	7,01	7,72	7,69	7,68
Bl. lact, mg %	—	—	—	—	—	—	9,45	9,35	9,83	9,83	38,14	37,58	26,72
Pl., lact, »	—	—	—	—	—	—	8,70	7,70	9,66	9,66	46,57	42,95	33,31
Pulse, n/min	36,89	36,88	88,17	82,11	—	—	38,39	39,75	35,56	35,56	113,39	111,50	109,50
Respir., n/min	18,89	18,29	71,42	62,11	—	—	19,92	23,25	17,75	17,75	91,39	81,00	76,63
Load/(tempo ¹)	—	—	69,8	76,1	—	—	—	—	—	—	120	121	136
Training degree	—	—	2,98	3,22	—	—	—	—	—	—	3,00	3,25	2,63
Weather	—	—	5,78	5,00	—	—	—	—	—	—	4,69	4,50	4,50

a > b = P < 0,05, ¹) Load = weight of the rider + saddle for riding horses, tempo sec/1 000 m during the last two minutes of the test for trotters, M = mares, G = geldings, S = stallions.

Table 5. Effect of disposition of riding horses and trotters on the blood values and pulse and respiration rates at rest and at peak stress

No. of cases	Riding horses						Trotters					
	At rest			At stress peak			At rest			At stress peak		
	Calm 40	Uneasy 8	Crazy 3	Calm 40	Uneasy 8	Crazy 3	Calm 20	Uneasy 12	Crazy 1	Calm 20	Uneasy 12	Crazy 1
Hb, g/100 ml	12,60 ^b	13,05	15,03 ^a	15,99	15,90	15,97	12,95 ^b	15,07 ^a	13,60	18,53	19,34	18,55
Hc, %	34,95 ^b	37,15	42,07 ^a	42,85	43,24	42,83	37,30	42,25	40,00	51,38	53,44	51,30
Glucose, mg %	101	97	95	95	93	82	104	98	105	104	106	97
Ca, mg %	12,64	12,58	12,82	12,09	12,09	12,28	11,76	11,83	11,00	11,19	11,17	10,85
Mg, »	1,80 ^a	1,82 ^a	1,66 ^b	1,71	1,74	1,69	1,80 ^c	1,84	2,10	1,75	1,77	2,15
P, »	3,34 ^a	3,49 ^a	2,86 ^b	3,88	3,74	3,25	3,54	3,29	3,87	4,37	4,17	5,02
K, mg %	17,00 ^b	17,35 ^b	19,37 ^a	19,09	19,22	19,83	17,82	18,71	10,50	19,07	19,20	17,80
Na, »	316	312	318	317	313	317	320	315	314	321	318	317
Fe, µg %	117	108	134	137	132	136	124	143	85	159	186	132
Cu, »	80	72	88	83	73	87	80	81	72	83	84	76
Zn, »	49	60	44	49	46	36	60	54	53	53	54	73
Tot. prot., g %	—	—	—	—	—	—	6,92	7,06	6,53	7,70	7,72	7,46
Bl. lact., mg %	—	—	—	—	—	—	9,49	9,91	9,10	30,77	36,77	17,80
Pl. lact., »	—	—	—	—	—	—	8,65	9,91	6,70	38,02	44,18	19,60
Pulse, n/min	36,75	37,25	48,67	87,80	84,25	86,00	36,25	38,58	39,00	110,90 ^b	109,67 ^b	138,00 ^a
Respir., n/min	17,75 ^b	18,50 ^b	26,67 ^a	70,10	72,50	63,33	18,25	20,83	21,00	83,80	83,50	60,00
Load/tempo f)	—	—	—	71,40	68,00	74,67	—	—	—	134 ^a	117 ^b	137
Training degree	—	—	—	2,95	3,25	3,33	—	—	—	3,05 ^a	2,50 ^b	3,00
Weather	—	—	—	5,53	6,13	4,67	—	—	—	4,55	4,50	6,00

a > b = P < 0,05, f) Load = weight of the rider + saddle for riding horses, tempo sec/1 000 m during the last two minutes of the test for trotters.

at peak stress. He died of a heart attack about an month after the test.

Plasma glucose levels did not change significantly during the physical stress test. In a previous study, glucose level of whole blood of riding horses decreased significantly as a result of physical stress, the extent of decrease being related to that of increase in the red blood cell content of the blood (TANHUANPÄÄ et al. 1976). In the present material horses which exhibited high elevations in lactic acid level failed to show significant changes in glucose levels as a result of physical stress. Of the blood parameters studied lactic acid (plasma and whole blood) level at peak stress seemed to be the best indicator of the physical condition of trotters. Riding horses failed to show marked increases in the lactic acid level due to the test, probably because the test was not strenuous enough.

On average, physical stress caused marked changes in the serum Ca/P of riding horses (from 3,79 to 3,17) and of trotters (from 3,40 to 2,55). Ca was the only cation in the plasma which decreased significantly due to physical stress. Inorganic phosphorus increased significantly. This phenomenon may be due to an increased rate in ATP breakdown during muscle work which results in liberation of phosphoric acid residue from the reaction: $ATP \rightarrow ADP + P$. Also Mg levels tended to decrease during stress. Both Ca and Mg are important, for instance in

heart and muscle functions, in maintaining muscle tonus. K and Fe increased significantly in plasma during physical stress. Presumably these cations are derived from the muscle cells and interstitial fluids, and possibly from red blood cells. Red cell destruction rate is likely to increase during strenuous physical work. Similarly, changes in acid-base balance in the plasma may cause changes in the concentrations of the various elements which maintain osmotic pressure in the blood.

Total protein content of plasma increased during the test although this increase was not significant. DE LANNE et al. (1958) have presented theories to explain this phenomenon. Plasma protein level increases during physical stress due to a decrease in plasma volume (PERSSON 1967). High respiration rate revealed the poor physical condition of several horses. With a planned training schedule, respiration rates in these horses could be significantly reduced.

The results of this study revealed among other things that the higher the speed of the horses tested the greater the changes observed in their blood composition. It is concluded that under constant test conditions, with standardized speed and load, well-trained, healthy, balanced and fast horses are likely to show less changes than untrained, unbalanced, slow or sick animals with aching feet, hips, back etc.

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SELOSTUS

Fyysisen rasituksen vaikutus pulssiin ja hengitystiheyteen sekä veren koostumukseen ratsuilla ja ravureilla

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Tarkoitukseen suunnitelluilla kokeilla testattiin 51 ratsumiehen ja 31 ravurin fyysinen kunto. Testeihin sisältyi pulssiin ja hengitystiheyden määrittämiset levossa, fyysisen rasituksen eri vaiheissa ja 10 min rasituksen päättymisestä. Hevosista otettiin verinäytteet levossa ja rasitushuipussa. Kokoverestä määritettiin hemoglobiini (Hb), hematokriitti (Hc) ja maitohappo, plasmasta määritettiin maitohappo, glukoosi, Ca, Mg, epäorg. P, K, Na, Fe, Cu, Zn ja kokonaisproteiini sekä levossa että rasituksessa.

Ravureilla oli nopeampi pulssi ja hengitystiheys ja rasitus aiheutti näillä suurempia muutoksia veren koostu-

muksessa kuin ratsuilla. Mitä nopeammin hevonen liikkui sitä enemmän Hb, Hc, glukoosi, Na, Cu, kokonaisproteiini ja maitohappo nousivat testin aikana. Valmennuksen aste, sääolot, ikä, sukupuoli ja hevosen luonne vaikuttivat tuloksiin. Tutkimus osoitti että jos koeolosuhteet, kuorman suuruus ja hevosen liikkumisnopeus ovat testatuilla hevosilla samat, niin hyvin treenatuilla, terveillä, tasapainoisilla, nopeilla hevosilla veren koostumuksen muutokset ovat vähäisemmät kuin treenattomilla, tasapainottomilla, hitailla ja sairailta hevosilla.

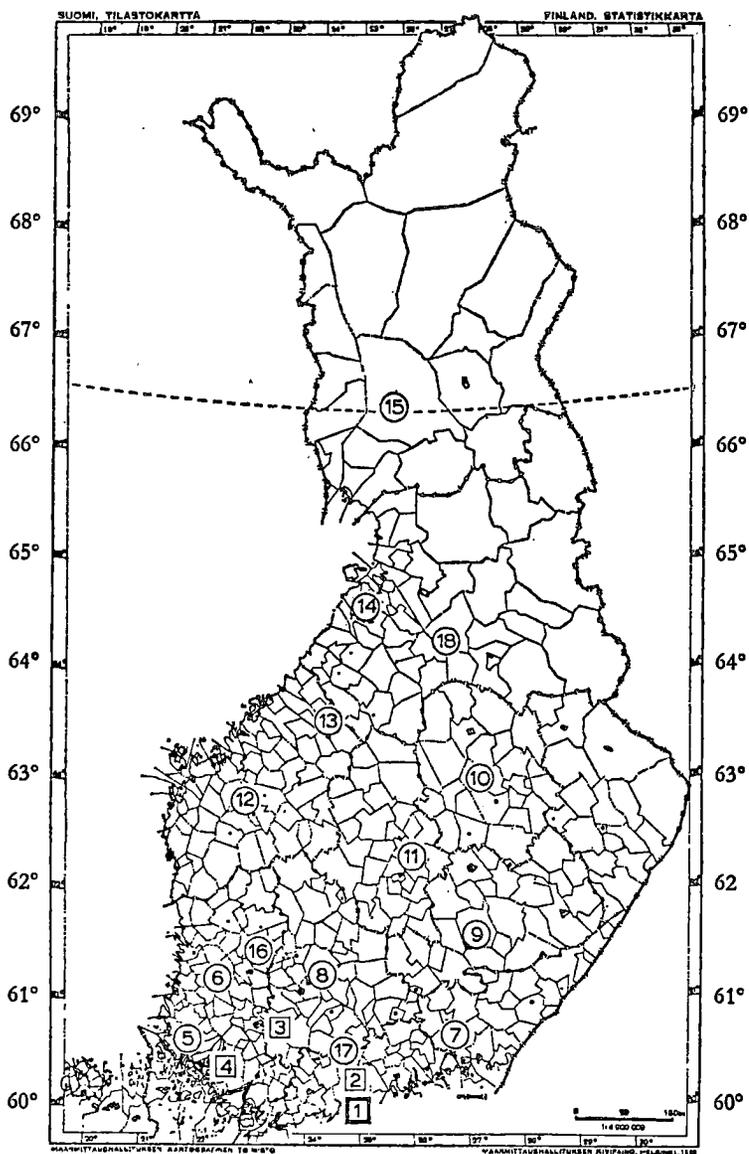
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2. SIPPOLA, J. Porvoo—Loviisa. Summary: Soil map of Porvoo—Loviisa. Agrogeol. Kartt. 29: 1—26+11 karttaa.



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