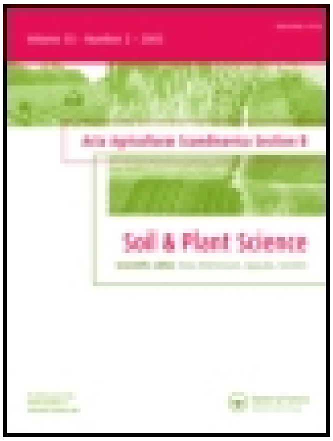

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Effect of genotype and environment on vegetative and reproductive characteristics of lingonberry (Vaccinium vitis-idaea L.)

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Effect of Genotype and Environment on Vegetative and Reproductive Characteristics of Lingonberry (*Vaccinium vitis-idaea* L.)

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A field experiment was carried out using cuttings and seedlings from 11 selected clones of lingonberry (*Vaccinium vitis-idaea* L.) planted at Balsgård, Sweden, in 1982. Daughter plants from two different clones and their corresponding seedling progenies were transferred to a Biothron at Alnarp, Sweden, in 1988. These two clones and their respective seedling populations were cultivated under conditions of controlled temperature and humidity, but in distinct environments with direct light and shade. Data on vegetative and reproductive growth were recorded. A small additional experiment to verify the effects of light on development was performed in frames at Alnarp. The results suggest that the genotype of wild lingonberry accessions controls their spreading ability (i.e. number of rhizomes), influences its growth, thereby affecting plant height, and determines the number of vegetative shoots, total number of shoots and berry set. Furthermore, light influences plant height, vegetative shoots and number of fertile shoots. The propagule system affects the number of both vegetative and fertile shoots. Plants derived from cuttings are superior to their corresponding seedling offspring, especially under shadow.

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Key words: genetic resources, influence of light, lingonberry, propagation, *Vaccinium vitis-idaea*.

Introduction

The first attempts to cultivate lingonberry began in Sweden and Finland in the 1960's (Teär, 1972; Fernqvist, 1977; Lehmushovi, 1977). An early interest in this new crop was also shown in Germany (Dierking and Krüger, 1984). Recent scientific work has been reported from the Nordic region (Gustavsson, 1993, 1996; Hjalmarsson, 1996; Saario and Voipio, 1997), other European states (Pliszka and Scibisz, 1989; Butkus et al., 1989) and North America (Stang et al., 1993a; Estabrooks, 1996; Penney et al., 1996). In addition to horticultural research, knowledge about this species was gained through ecological investigations (Tolvanen 1995; Fröborg, 1996 and others). The domestication of lingonberry is almost at the same stage as American blueberry in the early twentieth century (Galetta and Ballington, 1996).

Botanically the lingonberry plant is a perennial, evergreen dwarf shrub with underground rhizomes. The adventitious buds on the rhizome can either

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remain dormant or become activated and produce new underground stems or upright aerial shoots (Teär, 1972). Lingonberry can easily be propagated by seed if the derived seedlings are transplanted. Direct sowing in the field has been unsuccessful (Öster, 1974). In nature, lingonberry spread mainly through rhizomes (Ritchie, 1955) in a similar way to blueberry (*Vaccinium myrtillus*).

During early Swedish attempts to establish lingonberry plantations, different propagule systems were examined (Hjalmarsson, 1993). Plants derived from shoot cuttings cropped early, whereas seedlings derived from seeds spread fast. In choosing between these two propagules one should consider whether a seedling population would be less productive than a selected clone with the desired horticultural characteristics.

Until now, about a dozen lingonberry cultivars have been selected worldwide from wild-growing populations (Galetta and Ballington, 1996; Gustavsson, 1996). Significant variation in morphological characteristics and growth habit exists between and within populations assessed either in nature (Ritchie, 1955; Karlsson, 1982; Chester and Oechel, 1986; Tolvanen, 1995) or field experiments (Teär, 1972; Lehmushovi, 1986; Gustavsson, 1996; Estabrooks, 1996). Likewise, the phenotype of lingonberry accessions showed plasticity to environmental changes. However, the importance of genetic and environmental components of this variation has seldom been elucidated.

Early trials used wild populations, which would explain some of the contradictory results. For example, Eriksson et al. (1979) noted that the cover of lingonberry in Swedish pine forests was 8–9%, while for more compact spruce forest it was 4%, whereas in cultivated field experiments, Lehmushovi and Hiirsalmi (1973) found that shade (10–25% of complete illumination) increased the average shoot height. Conversely, Holloway et al. (1982), working with a specific clone in a controlled field experiment, reported more vegetative growth in full sunlight than under 44%, 56% and 73% shade. Tolvanen (1995) investigated aerial shoots (ramets) and observed architectural differences in growth habit between forest and open habitats. Teär (1972) compared the percentage of fertile shoots in different forest types and noted most fertile shoots (59%) in clear areas and least in spruce areas (27%). Kardell and Eriksson (1983) reported that berry yield was doubled after clear-cut. Hence, the objective of our investigation was to assess the influence of genotype, propagule system and light intensity on phenotypic characteristics of lingonberry.

Materials and methods

Origin of plant material

The plant material in the first two experiments originated from seed samples collected in the forest by the late Professor Sven Dalbro of the Royal Veterinary and Agricultural University (KVL, Denmark). The berries were picked from high yielding and large fruiting stands in the county of Småland (Sweden). The seed lot was sown at KVL's orchard Pometet (Tåstrup, Denmark) in 1977 and the seedlings were moved to a field at Balsgård, Sweden, where they were selected for vegetative growth, fruiting habit and plant health. Cuttings of the Dutch cultivar 'Koralle' were used in the third experiment at Alnarp, Sweden. The plant material was obtained from Wilhelm Dierking Beerenobst (Gilten, Germany). 'Koralle' is a bush-like cultivar ~30 cm tall when fully grown. It was marketed in 1969 by H. van der Smit from Reenwijk in Holland (Zillmer, 1984).

Definition of shoots

In this study, vegetative and fertile shoots were defined as terminal shoots either at the top of the main branch or on lateral branches. The term leafy rhizome shoots was used for shoots emerging from the mother plant rhizomes.

Experiment 1

Eleven of the most promising clones selected at Balsgård were propagated by cuttings and seeds. The new plants, representing first and second generation of the selected clones, were arranged in a field experiment at Balsgård in June 1982. Each population was transplanted into a plot with a minimum of 10 and a maximum of 100 individuals depending on the amount of available material. The number of plots for this experiment was 22, with a total of 1230 plants. The plots were arranged in two beds with a pathway between them. Planting distance within plots was 20 × 20 cm. The soil at the experiment site was sandy with low humus content. To improve growing conditions, a 5-cm layer of unfertilized, unlimed *Sphagnum* peat was mixed into the soil to a depth of 15 cm before planting in June 1982. General appearance, development of new shoots, and berry number were scored using a 1–9 (best) scale, while ground coverage of the plants was recorded as a percentage during 1984 and 1985. In addition, berry weight was recorded in 1984.

Experiment 2

Two clones (with high scores for the selection criteria) and their corresponding seedling progenies were selected at Balsgård for further observations in the Biothron at Alnarp. Individual plants from each of the four populations were dug up from the field at the end of 1987. The individual plants derived from outgrowth of the mother plant rhizomes. Most of them had only one main branch developed from the base, but occasionally there were two or three original branches. The plants were kept in a peat frame at Alnarp during the winter, and afterwards they were planted in 1.5 l pots and moved into the Biothron. This experiment was conducted from 1988 to 1992. The material was kept in the Biothron during the growing season (April–November) while the frame yard was used for winter storage (December–March). In the Biothron the pots were placed on wheeled carts. The table spaces of the carriages were 50 × 50 cm and the height was 90 cm. Twelve pots were placed on each table space. Every second cart was covered with cloth to provide 50% shadow. The cloth was attached like a squared tent (50 × 50 × 50 cm) on top of the table space. The shade frames were removed during winter (December–March). Garden peat was used as growing media and the plants were irrigated manually. Nutrition was given once a month during the summer period with a special fertilizer for calcifuges.

The growth chamber in the Biothron had natural daylight. Temperature and relative humidity were adjusted to prevailing values in the county of Småland according to the statistics of the Swedish Meteorological and Hydrological Institute.

The experiment was a completely randomized design, with two replicates of 12 plants per wheeled cart. Each wheeled cart had the combination clones × propagule system × light. Plant height was recorded sequentially in October 1988, June 1989, November 1989, May 1990 and May 1992. Vegetative and fertile shoot number and length were scored in October 1988 and November 1989, while number and length of leafy rhizome shoots were recorded in October 1988. Likewise, the number of flower clusters and flowers per cluster were counted in June 1988 and 1989.

Experiment 3

An additional experiment with 1-year-old uniform plants of the cultivar 'Koralle' was planted in a peat bed at Alnarp in July 1996. There were 12 plots with six plants per plot. Planting distance within plots was 20 × 20 cm. Every second plot was covered with a squared net tent (30 cm tall) providing 50% shadow. The remaining six plots were left untreated as control. The experiment was thus arranged as a completely randomized design with six replicates. The experiment finished in September 1997 when the plants were harvested. Above-ground biomass fresh weight, number and length of vegetative shoots, length of internodes on vegetative shoots, number and length of fertile shoots, length of internodes on fertile shoots and berry number per fertile shoot were recorded in this experiment.

Statistical analysis

Data from all three experiments were analysed by analysis of variance (ANOVA) using the MSTAT-C statistical program (Anon., 1989). Combined and individual analyses were carried out to examine the influence of genotype, propagule system and environment on morphological characteristics. Effects were tested using synthetic F-test according to Satterhwaite's approximation for experiments 1 and 2.

Results

Experiment 1

According to the ANOVA across years and clones irrespective of propagule system, the general appearance of plants was not influenced by accessions (i.e. clones including offspring) or year. The ground coverage and the development of new shoots depended significantly on accessions ($P < 0.05$). Accessions 34, 23 and 35 had the highest covering, while accessions 23 and 34 showed most new shoots (Table 1). The production of new shoots and berries was affected significantly by the year of assessment ($P < 0.01$). The interaction between accession and year was not significant ($P > 0.05$) for any characteristic.

When propagule systems (cuttings vs. seedlings of the same clone) were compared year by year (Table 2), significant differences were found in both 1984 and 1985 for percentage coverage and number of new shoots. Seedlings had greater coverage and more new shoots than plants derived from cuttings. Conversely, the latter had a greater number of berries, but this difference was only significant in 1984 ($P = 0.058$ for 1985). Differences in general appearance between propagule systems were non-significant, but in 1985 this characteristic depended significantly ($P = 0.039$) on the accessions.

Experiment 2

All characteristics, except length of fertile shoots, number of rhizome shoots and flowers per cluster, were significantly affected by the interaction between date of recording and treatment in the Biothron. Table 3 indicates the plant height of the two selected lingonberry accessions (23 and 34) grown at full daylight or under shadow using cuttings or seedlings at five different dates.

Table 1. Field assessment of characteristics of Swedish lingonberry accessions at Balsgård (1984 and 1985)

Accession number	General appearance[1]	Percentage coverage	New shoots[1]	Berry number[1]
3	6.00	58.75	5.00	5.50
12	6.50	61.25	4.00	5.75
23	6.75	66.25	5.75	5.00
27	5.00	46.25	3.50	4.75
34	6.00	67.50	6.25	5.25
35	6.75	66.25	5.00	6.25
37	4.75	55.00	4.00	4.25
38	4.50	47.50	4.50	3.50
39	4.75	52.50	4.50	3.50
40	6.50	50.00	5.00	6.75
41	6.50	52.50	4.75	5.75
Mean standard error	0.67	13.30	1.58	1.51

[1]Scale 1–9; 9 = best.

Significant differences between accessions were observed for plant height, total number of shoots, number of vegetative shoots and number of flowers per cluster in 1988 (Table 4). Accession 23 had taller plants (Table 3) with more shoots, but fewer flowers per cluster than accession 34. Light treatment influenced plant height (Table 3), vegetative shoot length and number of vegetative and fertile shoots (Table 4). Plants were taller and with more and longer vegetative shoots, but fewer fertile shoots, under shadow than when exposed to full daylight. The total number of shoots was almost the same ($P > 0.05$) irrespective of light treatment. There were significant differences between propagule systems (clones versus seedlings) for plant height (Table 3), total number of shoots, number of fertile shoots, number of rhizome shoots and number of flower clusters (Table 4). Vegetative propagation enhanced all these characteristics.

Interactions between accession and propagule system, and light and propagule system were significant ($P < 0.05$) for number of vegetative and fertile shoots (data not shown). Accession 23 had more vegetative shoots than accession 34, and this difference was larger in clones (~ 2) than seedlings (~ 0.4). Similarly, clones had more vegetative shoots than seedlings under shadow (6 versus 4), while both propagule systems had almost the same number of vegetative shoots (4) under daylight. More fertile shoots were always recorded with cuttings but these differences were greater under daylight. Finally, the interaction between accession and propagule system was significant ($P < 0.05$) for rhizome numbers. Cuttings from accession 23 had more rhizome shoots than those of accession 34, while this rhizome shoot number was equal in the seedling system.

Significant differences ($P < 0.05$) between accessions for plant height were confirmed during the following 3 years (Table 3). In 1989, the interaction between accession and propagule system was significant ($P < 0.05$), which indicated that the differences in height were larger in clones than seedlings. However, at the final recording (April 1992) plant height was not significantly affected by any factors or interactions.

In 1989, significant differences between accessions for number of vegetative shoots were also confirmed (Table 5). In addition accessions differed significantly for number of fertile shoots plus number and length of rhizome shoots. Accession 23 had the highest values for length of rhizome shoots, while the opposite was true for number of fertile shoots. A significant ($P < 0.05$) influence of light was observed in 1989 for number of fertile shoots and number of flower clusters. These were more abundant in plants exposed to full daylight. In addition, the propagule system had a significant effect on number of shoots (both vegetative and fertile), length of vegetative shoots and number of flower clusters. Clones had, as observed earlier, more fertile shoots than seedlings. There were significant differences ($P < 0.05$) for number and length of vegetative shoots plus number of flower clusters. Clones had more but shorter shoots and more flower clusters than seedlings.

Analysis of the interactions showed that the number of fertile shoots was significantly ($P < 0.05$) affected by all factors. The length of vegetative shoots and number of rhizome shoots were significant when tested against the interaction of light and propagule system. The length of the vegetative shoots was the same (31 mm) irrespective of propagule system under shadow, while the seedlings had longer vegetative shoots than the cuttings when their derived plants were exposed to daylight (34 and 26 mm, respectively). Cuttings had more rhizomes than seedlings

Table 2. Comparison of cutting versus seedling propagules at Balsgård

Propagule system		General appearance[1]	Percentage coverage	New shoots[1]	Berry number[1]
1984					
	Cuttings	6	38	4	7
	Seedlings	6	70	7	2
	Mean comparison	n.s.	***	***	***
1985					
	Cuttings	6	40	2	6
	Seedlings	6	79	7	5
	Mean comparison	n.s.	***	***	n.s.

[1]Scale 1–9; 9 = best.
n.s. and *** indicate non-significant or significant mean comparison at the 0.1% level of probability.

under shade (7.7 versus 3), while the opposite was true when their derived plants were exposed to daylight (5.8 and 6.7, respectively).

Experiment 3

The differences between daylight and 50% shade for above-ground biomass fresh weight and total number of shoots in the cultivar 'Koralle' were non-significant (Table 6). Also, the length of its vegetative shoots and internodes were unaffected. However, other characters differed significantly ($P < 0.05$). More fertile shoots and berries were produced when plants of 'Koralle' were exposed to full daylight, while fertile shoots, and their internodes, became significantly longer in shade.

Discussion

The general appearance of accessions was very similar across years irrespective of the propagule system. This result could be explained because the accessions for our research were chosen according to their attractive phenotypes and high yielding stands in the forest. The ability to cover the surface depended upon accessions, which suggested that spreading might be a characteristic influenced by the genotype. This observation was not surprising because Stang et al. (1993b) reported significant variation in the number of rhizomes and rhizome shoots between the cultivars 'Koralle' and 'Erntedanke'. Furthermore, Saario and Voipio (1997) observed greater ground coverage in the cultivar 'Sussi' than in the cultivar 'Sanna'. Likewise, Estabrooks (1996) indicated that during the fourth growing season plant spread varied from 20 cm to 57 cm in six selected seedlings of lingonberry grown from seeds collected in Canada.

The year of assessment significantly affected the production of new shoots and berries owing to alternate peak years for vegetative growth and flowering in lingonberry, as reported earlier by Tolvanen (1995). Plant age could be regarded as another factor affecting this characteristic. Plants derived from seedlings must have a juvenile phase before starting their reproductive stage. In our experiment the seedling plants were not fully reproductive until 1985.

Propagule systems (cutting or seedlings) affected percentage of ground cover of plants, shoot and berry number, which confirmed earlier reports by Lehmushovi and Säkö (1975) and Hjalmarsson (1993). Cutting propagules enhanced early cropping and uniform plantations, but had poor vegetative spreading capacity. Conversely, seedlings developed rhizomes very early and thus had an even ground cover.

General appearance differed significantly between accessions in old plants. This characteristic consists of plant health, height, architecture, foliage and berry set. Hence, our assessment suggested that these component characteristics were easily distinguished as the stands became older and larger.

Significant differences in plant height between accessions were observed during the early recording dates in the Biothron. For example, accession 23 had taller plants than accession 34 until the fourth date of recording but both accessions showed the same plant height at the end of the experiment. Therefore, genotype may affect growth rate rather than plant height itself. Lehmushovi (1986) found significant variability for plant height in 88 Finnish wild lingonberry accessions. The accessions were divided in 10 groups according to their geographical origin because plant height followed a north–south trend, i.e. accessions collected from the north were the tallest.

Table 3. Plant height (mm) of two selected lingonberry accessions (23 and 34) grown at full daylight (D) or under shadow (S) using cuttings (C) or seedlings (Sd) in a Biothron (Alnarp, 1988–1992)

	Accession		Light		Propagule		
Days after planting	23	34	S	D	C	Sd	SE[1]
180	130	88	116	102	116	102	3
420	127	91	113	105	124	94	4
570	167	137	158	146	160	144	5
750	175	152	166	161	162	165	4
1480	172	171	171	171	166	177	4

[1]Standard mean error.

The number of vegetative shoots as well as the total number of shoots depended on genotype. According to Teär (1972), the majority of new shoots within a lingonberry plant develop from 1-year-old sterile shoots, which could explain the observed association between these two characteristics.

The Biothron experiment confirmed that the number of rhizome shoots, i.e. the ability for spreading, depended on the genotype of the accession. Furthermore, significant variation between accessions for number of flowers per cluster and number of fertile shoots confirmed that both accessions differed in their productivity, as reported in our earlier field experiment.

Light influenced the phenotype for plant height, vegetative shoot length and the number of vegetative and fertile shoots. Plants were taller with more and longer vegetative shoots, but had fewer fertile shoots and flower clusters under shadow. Thus, the total number of shoots depended on the genotype, but the development of their vegetative or fertile shoots depended on sunlight, i.e. long vegetative shoots were developed under shadow, while light enhanced the production of fertile shoots. These findings were in accordance with earlier reports by Teär (1972) and Tolvanen (1995). Both authors found that lingonberry plants in open habitats were shorter and showed a more sympodial branching system than plants from the forest. In addition, Tolvanen (1995) stated that the total number of vegetative buds was the same in both sites.

The two propagule systems affected plant height, total number of shoots, and number of flower clusters. Vegetative propagation enhanced all these characteristics, suggesting that clonal propagules were superior to their corresponding seedlings. The interactions accession × propagule and light × propagule significantly affected the number of vegetative shoots, which suggested that the influence of propagule system in the phenotype of this characteristic differed according to each accession, and that how light influenced the number of vegetative shoots depended on the propagule system. Hence, stronger plants were derived from cuttings and their superior vegetative development was enhanced under shadow compared with their corresponding seedling offspring.

Accession 23 had more rhizomes than accession 34 in the cutting system, while both had almost the same number in the seedling system. Also, in 1989 under shadow plants of accession 23 had more rhizomes than those plants of accession 34. Therefore, offspring derived from seedlings showed lower spreading ability than those from cuttings, especially in shaded habitats. Furthermore, both vegetative propagation and light enhanced the number of fertile shoots. Thus, light must be an important factor for colonizing new habitats by lingonberry seedlings. In 1989 the number of fertile shoots was significantly affected by all the factors and interactions. This result indicated that the phenotype of this characteristic was influenced by both the genotype of the accession and the environment where the accession was grown.

Daylight and partial (50%) shading did not significantly affect above ground biomass in the cultivar 'Koralle'. Our findings disagreed with those reported earlier by Holloway et al. (1982), who found that biomass (including the weight of underground rhizomes and roots) was significantly higher without shade after three growing seasons in an Alaskan site.

Light did not affect the total number of shoots in cultivar 'Koralle' as reported earlier in our experiment with selected wild lingonberry accessions. Thus, this characteristic depended solely on the genotype. The results for length of vegetative shoots differed also between selected wild accessions and 'Koralle'. Vegetative shoots were longer under shadow only for selected wild lingonberry accessions grown in the Biothron. Furthermore, 'Koralle' had 72% fertile shoots in our experiment, while fertile shoots in Swedish forests normally vary between 1% and 29% (Teär 1972). Full daylight enhanced the number of fertile shoots and berry set in 'Koralle', as indicated earlier in this series of experiments with wild germ plasm. The low level of available photosynthates

Table 4. Morphological characteristics of two selected lingonberry accessions grown using cuttings (C) or seedlings (Sd) at full daylight (D) or under shadow (S) in a Biothron (Alnarp, 1988)

	Accession		Light		Propagule		
Characteristic	23	34	S	D	C	Sd	SE[1]
Total shoots (#)	11	7	8	10	11	6	1
Vegetative shoot length (mm)	28	28	33	23	28	29	1
Vegetative shoots (#)	6.1	3.2	5.1	4.2	5.0	4.2	0.3
Fertile shoot length (mm)	32	29	33	28	31	30	1
Fertile shoots (#)	1.7	2.0	0.5	3.3	2.8	0.9	0.3
Rhizome shoots (#)	3.0	1.8	2.0	2.8	3.5	1.3	0.4
Flower clusters (#)	2.0	2.8	2.4	2.4	3.6	1.3	0.4
Flowers/cluster (#)	6.1	7.3	6.4	7.0	6.9	6.5	0.3

[1]Standard mean error.

Table 5. Morphological characteristics of selected lingonberry accessions grown using cuttings (C) or seedlings (Sd) at full daylight (D) or under shadow (S) in a Biothron (Alnarp, 1989)

	Accession		Light		Propagule		
Characteristic	23	34	S	D	C	Sd	SE[1]
Total shoots (#)	38	31	28	41	44	25	2
Vegetative shoot length (mm)	32	29	31	30	29	32	1
Vegetative shoots (#)	25.0	14.5	18.1	21.4	24.2	15.3	2
Fertile shoot length (mm)	29	28	26	31	29	28	2
Fertile shoots (#)	6.2	11.5	3.6	14.1	12.0	5.8	0.7
Rhizome shoots (#)	7.1	4.5	5.3	6.3	6.8	4.9	0.8
Rhizome shoot length (mm)	66.0	39.1	50.7	54.4	57.8	47.3	3.3
Flower clusters (#)	1.5	2.5	0.5	3.5	3.2	0.8	0.4

[1]Standard mean error.

Table 6. Influence of light in the development of the cultivar 'Koralle' at Alnarp (1997)

Characteristic	Shadow	Light	Mean comparison
Biomass fresh weight (g)	23	29	n.s.
Fertile shoots (#)	21	37	*
Fertile shoot length (mm)	45	34	**
Fertile shoot internode (mm)	4	3	**
Berry/fertile shoot	4	6	*
Vegetative shoots (#)	24	18	*
Vegetative shoot length (mm)	58	56	n.s.
Vegetative shoot internode (mm)	6	5	n.s.
Total shoots (#)	46	55	n.s.

n.s., non-significant mean comparison.
Significant mean comparison at *5% and **0.1%.

from the leaf may be another factor that negatively affects the number of fertile shoots.

Our research shows the importance of genotype, propagule system and light intensity in lingonberry growth and development. Hence, all these factors should be considered when developing a strategy for conserving lingonberry genetic resources in both genebanks and in situ reserves.

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