Semiflexible chains under tension

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A functional integral formalism is used to derive the extension of a stiff chain subject to an external force. The force versus extension curves are calculated using a mean-field approach in which the hard constraint $\mathbf{u}^2(s)=1$ is replaced by a global constraint $\langle \mathbf{u}^2(s)\rangle=1$ where $\mathbf{u}(s)$ is the tangent vector describing the chain and s is the arclength. The theory *quantitatively* reproduces the experimental results for DNA that is subject to a constant force. We also treat the problems of semiflexible chain in a nematic field. In the limit of weak nematic field strength our treatment reproduces the exact results for chain expansion parallel to the director. When the strength of the nematic field is large, a situation in which there are two equivalent minima in the free energy, the intrinsically mean-field approach yields incorrect results for the dependence of the persistence length on the nematic field. © *1997 American Institute of Physics.* [S0021-9606(97)51310-9]

I. INTRODUCTION

Inspired by the elegant experiments by Smith *et al.*[1] on the response of DNA to stetching by a constant force, few theoretical papers[2–5] have considered the effect of external field on semiflexible chains. Since DNA is stiff it can be described, at least approximately, as a worm-like chain. The eariest theoretical paper dealing with this problem was initiated by Fixman and Kovac.[2] These authors used a modified version of the Gaussian model for stiff chains and provided expressions for the stretching as a function of applied force. Their treatment is only valid when the applied force is small and significant deviation from these predictions are observed at sufficiently large values of the external force. Marko and Siggia[3] have calculated the extension as a function of force for worm-like chains and found that their results fit the experimental data very well. Some aspects of this theory have also been considered by Odijk[5] who also discusses the competition between entropically dominated effects and elasticity effects.

In this paper we revisit the problem of a semiflexible chain subject to tension. A functional integral formalism together with a mean-field treatment allows us to set up a general way of tackling problems involving semiflexible chains. When our theory is applied to the case of stretching of DNA by a constant force, we obtain excellent agreement with experimental results for the force versus extension.

II. ELASTIC RESPONSE OF A SEMIFLEXIBLE CHAIN

A. Mean-field theory

The simplest model for a semiflexible chain (SC) is obtained by taking into account the persistence in the tangential direction. A SC can be described by a space curve $\mathbf{r}(s)$ of total contour length L with s being the arclength. The unit tangent vector is $\mathbf{u}(s)\equiv\partial\mathbf{r}(s)/\partial s$ with the constraint that $\mathbf{u}^2(s)=1$ for all s. Since the molecule is stiff it costs energy to bend and the bending energy per segment length is proportional to $(\partial u(s)/\partial s)^2$. The difficulty with calculations involving this formulation of SC is that one has to invoke the constraint that $\mathbf{u}^2(s)=1$. This makes even the free-chain problem nonlinear. There has been extensive treatment of models of SC in the literature.[6–15]

Now consider applying an external field that stretches the chain. The effective free-energy can be written as

$$F=-k_BT\ \ln Z, \tag{1a}$$

where

$$Z=\int \mathscr{D}[\mathbf{u}(s)]\delta(\mathbf{u}^2(s)-1)e^{-\mathscr{H}/k_BT} \tag{1b}$$

with

$$\frac{\mathscr{H}}{k_BT}=\frac{l_p}{2}\int\left(\frac{\partial\mathbf{u}(s)}{\partial s}\right)^2 ds-\int \mathbf{f}(s)\cdot\mathbf{u}(s)ds. \tag{1c}$$

In Eq. (1c) l_p is the persistence length of the semiflexible chain (which in the experiments of Smith *et al.*[1] on DNA is estimated to be 53 nm). For generality we have assumed that the external field $\mathbf{f}(s)$ depends on the arclength s. The case of uniform $\mathbf{f}(s)=\mathbf{f}$ is appropriate for the experiments of Smith *et al.* and is the one treated in the previous theoretical papers. In particular Marko and Siggia[3] have used an eigenfunction expansion to obtain the extension versus f by exploiting the analogy between this problem and the quantum problem of a dipolar rotor in an external electric field.

Here we use a mean-field approach[6,9] that effectively replaces the local constraint $\mathbf{u}^2(s)=1$ by a global one $\langle\mathbf{u}^2(s)\rangle=1$. Such a theory has been shown to give an exact expression for the mean end-to-end distance of SC when $\mathbf{f}(s)=0$.[6] The basic idea is to enforce the constraint $\mathbf{u}^2(s)=1$ using an auxillary field variable $\lambda(s)$ and evaluate the resulting integrals over $\lambda(s)$ by the stationary phase approximation. The free energy [cf. Eq. (1)] can be rewritten as

$$\exp(-F/k_BT)=\int_{-i\infty}^{i\infty}\mathscr{D}[\lambda(s)]\int\mathscr{D}[\mathbf{u}(s)]\Psi[\mathbf{u}(s),\mathbf{f}(s)]\times\exp\left[\int_0^L\lambda(s)ds\right]+\text{const}$$
$$=\int_{-i\infty}^{i\infty}\mathscr{D}[\lambda(s)]\exp\{-\mathbf{F}[\lambda,\mathbf{f}(s)]\}+\text{const}, \tag{2a}$$

where

$$\Psi[\mathbf{u}(s),\mathbf{f}(s)]=\exp\left[-\frac{1}{2}\int_0^L\int_0^L\mathbf{u}(s)Q(s,s')\mathbf{u}(s')+\int_0^L\mathbf{u}(s)\cdot\mathbf{f}(s)ds\right] \tag{2b}$$

and

$$\mathscr{F}[\lambda(s),\mathbf{f}(s)]=-\ln\int\mathscr{D}[\mathbf{u}(s)]\Psi[\mathbf{u}(s),\mathbf{f}(s)]-\int_0^L\lambda(s)ds \tag{2c}$$

with

$$Q(s,s')=\left[-l_p\left(\frac{\partial}{\partial s}\right)^2+2\lambda(s)\right]\delta(s'-s). \tag{2d}$$

The constants in Eq. (2a) come from normalizations associated with $\mathscr{D}[\lambda(s)]$ and $\mathscr{D}[\mathbf{u}(s)]$. These constants will be omitted from now on.

The function $\mathscr{F}[\lambda(s),\mathbf{f}(s)]$ is a generating functional which can be used to calculate various correlation functions. For example the connected correlation function

$$\langle\mathbf{u}(s)\cdot\mathbf{u}(s')\rangle_c=\langle\mathbf{u}(s)\cdot\mathbf{u}(s')\rangle-\langle\mathbf{u}(s)\rangle\cdot\langle\mathbf{u}(s')\rangle \tag{3a}$$
$$\equiv-\frac{\partial}{\partial\mathbf{f}(s)}\cdot\frac{\partial\mathscr{F}}{\partial\mathbf{f}(s')} \tag{3b}$$
$$=3Q^{-1}(s,s'). \tag{3c}$$

Similarly $\Delta R^2=\langle R^2\rangle-\langle R\rangle^2$ can be written as

$$\Delta R^2=\int_0^L ds\int_0^L ds'\,\frac{\partial}{\partial\mathbf{f}(s)}\cdot\frac{\partial\mathscr{F}}{\partial\mathbf{f}(s')}. \tag{4}$$

By performing the functional integrations with respect to $\mathbf{u}(s)$ the free-energy $\mathscr{F}[\lambda(s),\mathbf{f}(s)]$ can be written as

$$\mathscr{F}[\lambda(s),\mathbf{u}(s)]=\tfrac{3}{2}\ln Q-\tfrac{1}{2}\int_0^L ds\int_0^L ds'\mathbf{f}(s)\times Q^{-1}(s,s')\mathbf{f}(s')-\int_0^L\lambda(s)ds. \tag{5}$$

The variable $\lambda(s)$, that enforces the constraint $\mathbf{u}^2(s)=1$, is evaluated by stationary phase approach.[6,9] The stationary phase condition is obtained by requiring that $\partial\mathscr{F}/\partial\lambda(s)$ be an extremum. This leads to the equation

$$\frac{3}{2}\left(\frac{2}{Q}\right)_{s,s}+\int_0^L ds'\int_0^L ds''\mathbf{f}(s')Q^{-1}(s,s')\times Q^{-1}(s,s'')\mathbf{f}(s'')=1. \tag{6}$$

The value of $\lambda(s)$ that makes $\mathscr{F}[\lambda,\mathbf{f}(s)]$ stationary depends on the precise form of $\mathbf{f}(s)$. We now specialize to the condition that $\mathbf{f}(s)=\mathbf{f}=$const, independent of s. This is the situation that has been treated in the literature and is assumed to be relevant to the experiments of Smith *et al.*[1] For constant $\mathbf{f}$ the stationarity condition [Eq. (6)] gives a uniform value for λ. More precisely Eq. (6) reduces to

$$\frac{3}{2}\left(\frac{1}{-(l_p/2)(\partial/\partial s')^2+\lambda}\right)_{s,s}+\frac{f^2}{4\lambda^2}=1. \tag{7}$$

In order to evaluate the first term in Eq. (7) in a transparant manner we use the boundary condition $\mathbf{u}(0)=\mathbf{u}(L)$ and $\partial u(0)/\partial s=\partial u(L)/\partial s$. These conditions were implicitly assumed in Eq. (2b). The easiest way to compute the first term in Eq. (7) is in terms of an eigenfunction expansion. Let $\{|s\rangle\}$ denote the eigenstate with s the curvilinear space label and let $\{|n\rangle\}$ be the states that are Fourier conjugate to $\{|s\rangle\}$ in such a way

$$\frac{\partial|n\rangle}{\partial s}=i\left(\frac{2\pi n}{L}\right)|n\rangle. \tag{8}$$

The states $|n\rangle$ are eigenstate of ''momentum'' such that $\langle n|s\rangle=1/\sqrt{L}\,\exp(i2\pi ns/L)$. In terms of these eigenstates the first term in Eq. (7) becomes

$$\frac{3}{2}\left(\frac{1}{-(l_p/2)(\partial/\partial s')^2+\lambda}\right)_{s,s'}=\frac{3}{2}\langle s|\left(\frac{1}{-(l_p/2)(\partial/\partial s')^2+\lambda}\right)|s\rangle$$
$$=\frac{3}{2}\left(\frac{1}{-(l_p/2)(\partial/\partial s')^2+\lambda}\right)\sum_{n=-\infty}^{\infty}|n\rangle\langle n|s\rangle$$
$$=\frac{3}{2}\sum_{n=-\infty}^{\infty}\left(\frac{1}{\lambda L+(l_p/2)[(2\pi n)^2/L]}\right). \tag{9}$$

If we use the identity

$$\sum_{n=1}^{\infty}\frac{\cos nx}{n^2+\alpha^2}=\frac{\pi}{2\alpha}\cdot\frac{\cosh\alpha(\pi-x)}{\sinh\alpha\pi}-\frac{1}{2\alpha^2}. \tag{10a}$$

the stationarity condition for λ becomes

$$\frac{3}{4}\sqrt{\frac{2}{l_p\lambda}}\coth\left(\frac{1}{2}\Omega L\right)+\frac{f^2}{4\lambda^2}=1 \tag{10b}$$

with $\Omega=\sqrt{2\lambda/l_p}$. For large L Eq. (10b) simplifies to

$$1-\frac{3}{4}\sqrt{\frac{2}{l_p\lambda}}=\frac{f^2}{4\lambda^2}. \tag{10c}$$

As $f\to0$ this stationarity condition coincides with the one derived previously.

B. Correlation function and mean-square internal distance

In terms of the stationarity solution of λ, the various correlation functions can be computed. For example

$$\langle \mathbf{u}(s)\cdot\mathbf{u}(s')\rangle = 3Q^{-1}(s,s') + \frac{f^2}{4\lambda^2} = \frac{3}{4}\sqrt{\frac{2}{l_p\lambda}}\frac{\cosh[(L-2|s'-s|)\Omega/2]}{\sinh(\Omega L/2)} + \frac{f^2}{4\lambda^2}. \tag{11}$$

For $s=s'$ the above equation reduces exactly to the stationarity condition for λ [cf. Eq. (10b)] leading to $\langle \mathbf{u}^2(s)\rangle = 1$. Thus our approach ensures that the constraint $\mathbf{u}^2(s)=1$ is satisfied globally. For $L\Omega\to\infty$ Eq. (11) becomes

$$\langle \mathbf{u}(s)\cdot\mathbf{u}(s')\rangle = \frac{3}{4}\sqrt{\frac{1}{l_p\lambda}}\, e^{-|s'-s|\Omega} + \frac{f^2}{4\lambda^2}. \tag{12}$$

The mean-squared internal distance of the semiflexible chain under tension can be obtained as

$$\langle |\mathbf{r}(s')-\mathbf{r}(s)|^2\rangle = \int_s^{s'} ds_1 \int_s^{s'} ds_2 \langle \mathbf{u}(s_1)\cdot\mathbf{u}(s_2)\rangle. \tag{13}$$

Substituting Eq. (12) in Eq. (13) yields

$$\langle |\mathbf{r}(s')-\mathbf{r}(s)|^2\rangle = \int_s^{s'}\int_s^{s'} \langle \mathbf{u}(s_1)\cdot\mathbf{u}(s_2)\rangle ds_1\, ds_2 = \frac{3}{4}\sqrt{\frac{2}{l_p\lambda}}\left[\frac{2}{\Omega}\left|s'-s\right| - \frac{2}{\Omega^2}\left(1-e^{-\Omega|s'-s|}\right)\right] + \frac{f^2}{4\lambda^2}(s'-s)^2. \tag{14}$$

The above equation naturally suggests a length scale, l_f, below which entropy factors dominate and above which the mechanical energy associated with the orienting field dominates. For small values of the contour length $l=|s'-s|$ the field-dependent term becomes negligible whereas for long l the third term in Eq. (14) dominates. A scale l_f is obtained by balancing the first and last terms of Eq. (14) and is given by

$$l_f = \frac{3\lambda(f)}{f^2}. \tag{15}$$

When $fl_f \ll 1$ then the stationary phase condition can be easily solved and one gets $\lambda(f)\sim 1/l_p$ and consequently Eq. (15) becomes $l_f \sim 1/f^2 l_p$. Under these conditions one can think of the semiflexible chain to break up into a sequence of ''blobs'' of effective segment length given by

$$\xi_f \sim f^{-1}. \tag{16}$$

The above result coincides with the blob size predicted by flexible chain under tension.[16] The above blob length is called *tensile screening length*.[16] For Eq. (16) to be valid it is necessary that within the length ξ_f there should be a large number of segments each of length l_p. Since the effect f within ξ_f is negligible the chain on this length behaves effectively as a Gaussian chain containing l_f/l_p units. It is for this reason ξ_f in the law f limit coincides with the Pincus blob length. In the limit of $l_f f\to\infty$, Eq. (15) gives $l_f\sim 1/f$ and hence the chain conformation is dictated by coupling to the mechanical energy. In this limit we expect the chain to be aligned with the external field with almost complete suppression of fluctuations. The effect of f is felt at all length scales, i.e., l_f is effectively zero.

C. Average chain extension

The quantity of experimental interest is the average extension z of the chain parallel to the external field. The average elongation z is computed using

$$z = \left\langle \int_0^L \mathbf{u}(s)\cdot\frac{\mathbf{f}}{|\mathbf{f}|}\right\rangle. \tag{17}$$

The statistical average in Eq. (17) can be conveniently expressed in terms of the free-energy functional $\mathcal{F}$. When $\mathbf{f}$ is uniform we get

$$z = \frac{\mathbf{f}}{|\mathbf{f}|}\cdot\frac{\partial\mathcal{F}}{\partial\mathbf{f}} = f\int_0^L\left[-l_p\left(\frac{\delta}{\delta s}\right)^2 + 2\lambda(f)\right]^{-1} ds = \frac{fL}{2\lambda(f)}. \tag{18}$$

In Eq. (18) we have shown the argument of λ to emphasize the dependence of λ on f. The above equation and the associated stationarity condition [cf. Eq. (10c)] determines the average chain extension.

The chain extension z can be easily calculated for the case of $l_p f\to 0$ and for $l_p f\to\infty$. When $l_p f\to 0$ we get

$$z = f\frac{R_0^2}{3}, \tag{19}$$

where $R_0^2 = 2l_0 L = 2(2/3l_p)L$ is the size of the corresponding ideal chain with $l_0 \equiv 2/3l_p$ the mean-field persistence length.[6] The above result is also obtained for a Gaussian chain under tension. The leading-order correction to Eq. (19) can be obtained for $l_p f \ll 1$ by expanding Eq. (18) in power of f. The stationarity condition for $\lambda(f)$ up to $\mathcal{O}(f^2)$ becomes

$$\lambda(f) \approx \lambda_0 + \frac{f^2}{2\lambda_0^2}, \tag{20}$$

where λ_0 is the stationary phase condition for $f=0$.[6] Thus the average elongation becomes

$$\frac{z}{L} \approx f l_0\left(1 - \frac{8}{9}f^2 l_0^2\right). \tag{21}$$

In the small f limit the entropy considerations dominate the effects due to the orienting field.

The dependence of z on f is quite different in the opposite limit. If $fl_p\sim 1$ then we expect the external field to be relevant at all length scales. This would suppress the chain fluctuations on scale greater than l_p. When $l_p f\to\infty$ the sta-

tionary phase condition for λ has a solution $\lambda^{-1}\sim 0$ resulting in $\lambda = 1/2f$ [cf. Eq. (10c)]. In this limit $z/L \to 1$ and the chain assumes a rod conformation. In the limit of $l_p f \gg 1$ we can approximately solve Eq. (10c) to get

$$\lambda(f) \approx \frac{1}{2} f\left(1+\frac{3}{4}\sqrt{\frac{1}{l_p f}}\right). \tag{22}$$

The chain extension in the limit of large f becomes

$$\frac{z}{L} \approx \left(1-\frac{3}{4}\sqrt{\frac{1}{l_p f}}\right). \tag{23}$$

This result has already been noted in the literature.[5] The $f^{-1/2}$ behavior for semiflexible chains is in contrast to the Gaussian case. Apart from a numerical factor, the result in Eq. (23), valid for $l_p f \gg 1$, coincides with that discussed recently by Odijk[5] for semiflexible chains near the rod limit. The prefactor in front of $1/\sqrt{l_p f}$ obtained by Odijk is 1/2 which is slightly smaller than our result. The reason may lie in the fact that our treatment utilizes a stationary phase method to enforce the hard constraint $\mathbf{u}^2(s)=1$ globally.

In the limit of $l_p f \gg 1$ the chain fluctuations are relatively small and can be expanded in terms of $\theta_f \equiv (\theta_x, \theta_y)$ where θ_f is the angle between the tangent vector and the external field. The average extension is related to $\langle \theta_f^2(s)\rangle$ as

$$\frac{z}{L} \approx 1-\frac{1}{2}\langle \theta_f^2(s)\rangle. \tag{24}$$

For the uniform field we expect $\langle \theta_f^2(s)\rangle$ to be independent of s hence $\langle \theta_f^2(s)\rangle \equiv \langle \theta_f^2\rangle$. Comparing Eq. (23) we get an estimation of the mean fluctuations

$$\langle \theta_f^2\rangle = \frac{3}{2}\sqrt{\frac{1}{l_p f}} \tag{25}$$

which also coincides with the result of Odijk[5] apart from the numerical factor.

In addition to yielding the results reported in the literature our theory offers a simple estimate of the extension z/L as a function of f for arbitrary values of f. This is achieved by simultaneously solving Eqs. (10c) and (18). As a test of the utility of the stationary phase approach we compare our theory with the experiments of Smith *et al.*[1] on DNA. Marko and Siggia[3] have already shown that their numerically exact force extension for the semiflexible chain yields excellent agreement with experiments. In Fig. 1 we plot z versus f using the parameters appropriate for DNA. For comparison a few points from the experiments, as presented in Fig. 1 of Ref. 3, are also shown. The mean-field approach reproduces the data quantitatively.

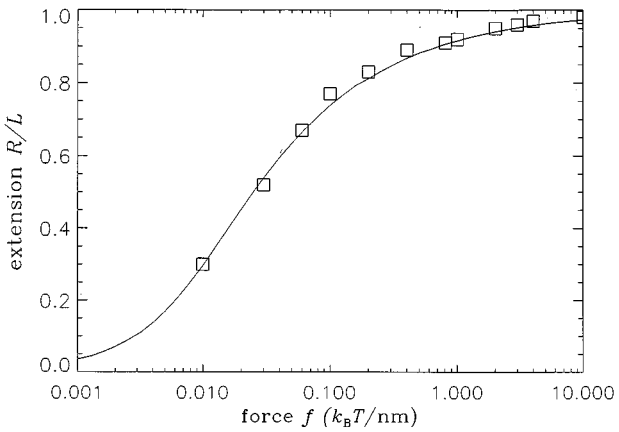

FIG. 1. The solid line is the force-extension curve obtained by simultaneously solving Eqs. (10c) and (18). The parameters have been chosen from the fit of force-extension curve for DNA reported by Smith *et al.* (Ref. 1). The value of $L=32.9$ μm and $l_0=53$ nm. The square represents the experimental results of Smith *et al.* as reported in Refs. 1 and 3.

III. CONCLUSIONS

In this article we have considered the problem of semiflexible chain subject to an external field using a functional integral formalism. The crux of our method hinges on replacing the local constraint that $\mathbf{u}^2(s)=1$ by a global constraint $\langle \mathbf{u}^2(s)\rangle = 1$ where $\mathbf{u}(s)$ is the tangent vector. The intrinsically mean-field approach has been shown to be successful in producing the configurational properties of semiflexible chains in the absence of the external field.[6,7,9] Here we have shown that the stationary phase method of enforcing the global constraint yields excellent results even when the chain is subject to tension. The very good agreement between the theory and the experiments on DNA subject to force is a confirmation of this assertion.

The approach we have described here is systematic but is not without limitations. These limitations become evident by considering the behavior of a semiflexible chain in a nematic environment, a problem that has received considerable attention in the literature.[17–22] A mean-field Hamiltonian of a stiff test chain in a matrix of other chains in a nematic state can be written as[19a]

$$\mathcal{H} = \frac{1}{2}\int_0^L\int_0^L ds\, ds'\, \mathbf{u}(s)Q(s,s')\mathbf{u}(s') - g\int_0^L u_z^2(s)ds, \tag{26}$$

where $\mathbf{u}(s)=[u_\perp(s), u_z(s)]$ and g (with the dimension of length) is the strength of the nematic potential. By following the procedure outlined in the previous section the stationary equation [one that extremizes the free energy with Eq. (26) as the Hamiltonian] becomes

$$1 = \frac{1}{2}\sqrt{\frac{2}{l_p\lambda}} + \frac{1}{4}\sqrt{\frac{2}{l_p(\lambda-g)}}. \tag{27}$$

The above equation ensures that

$$1 = \langle \mathbf{u}_\perp^2(s)\rangle + \langle u_z(s)\rangle = \langle \mathbf{u}^2(s)\rangle$$

instead of $\mathbf{u}^2(s)=1$ for all s. The mean extention of the chain parallel and perpendicular to the director axis can be calculated as

$$\langle R_\perp^2 \rangle = \int_0^L \int_0^L \langle \mathbf{u}_\perp(s) \cdot \mathbf{u}_\perp(s') \rangle ds\ ds' \tag{28a}$$

$$\langle R_z^2 \rangle = \int_0^L \int_0^L \langle u_z(s) \cdot u_z(s') \rangle ds\ ds'. \tag{28b}$$

Consider the weak nematic limit, i.e., $g \to 0$. For small g the stationary condition can be solved and the results can be used to get $\langle R_\perp^2 \rangle$ and $\langle R_z^2 \rangle$. These lead to

$$\frac{\langle R_\perp^2 \rangle}{2/3(2l_0L)} \approx 1 - \frac{1}{3} g l_0, \tag{29a}$$

$$\frac{\langle R_z^2 \rangle}{1/3(2l_0L)} \approx 1 + \frac{1}{3} g l_0, \tag{29b}$$

where $l_0 = 2/3 l_p$. The persistence length along the nematic field is increased by a factor of $(1+1/3gl_0)$ which compares well with the exact results (in the limit of $L \to \infty$) of Warner *et al.*[17]

A similar analysis for $g \to \infty$ suggests that chain fluctuations perpendicular to the director are totally suppressed whereas the persistence length along the director is predicted to increase by a factor of 2. This result is in contrast with the analysis of several authors[17,19a,21] who have shown that the effective persistence length grows exponentially as $(gl_p)^{1/2}$. The nematic potential, $-gu_z^2$, has two deep minima at large g at $u_z = \pm 1$. Thus in the large g limit the chain configuration is dominated by ''tunneling'' between the two minima by an instanton.[22] Mathematically the partition function is dominated by instanton contributions which our mean-field theory fails to capture. It is clear that if there is symmetry breaking in the problem then the replacement of the hard constraint by a global one can lead to incorrect results.

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